CENTRAL AFRICAN LOWLAND FOREST RESILIENCE TO FIRE DISTURBANCE AND CLIMATE CHANGE: ANSWERS FROM THE PAST

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THESIS ABSTRACT

Central African lowland forest resilience to fire disturbance and climate change: answers from the past

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Thesis submitted for the degree of Doctor of Philosophy (DPhil), Trinity term 2015.

Tropical rainforests have been and will remain subjected to various natural and human pressures, which have already led to rainforest degradation and disappearance. This thesis aims to improve our current knowledge of the likely future trajectory of the persistence of the tropical African rainforest under climate change and fire impact through reconstruction of past vegetation and burning dynamics using palaeoecological records from sedimentary sequences.

I used several types of palaeoecological proxies (i.e., fossil charcoal, phytolihs, and fossil pollen) from sediment records collected in the Sangha River region, in the northern part of the Republic of Congo, to explore past fire dynamics between four different forest types (i.e. mixed forest, swamp forest, Marantaceae forest and monodominant *Gilbertiodendron* forest), and to reconstruct the vegetation history of two endemic types of African forest i.e., the Marantaceae forest and the monodominant *Gilbertiodendron* forest, for the last 2500 cal BP. Lastly, I combined fossil pollen records from the literature with ecological niche models (ENM) to explore the relationship between climate and rainforest distribution over the last 6000 cal BP.

My results demonstrate that the past frequency of predominately human-induced fires was significantly higher in areas currently covered by Marantaceae forest compared to areas currently covered by any of the other forest types, and that this high frequency of fires has therefore contributed to the maintenance of Marantaceae forest. Thus, the two Marantaceae forest sites I studied are of recent formation (around 450-600 cal BP) and were previously covered by the mixed forest type. Out of all the considered forest types, the mixed forest is the most vulnerable to both climatic and fire disturbances while the monodominant *Gilbertiodendron* forest has been most resilient to past climatic events, with no major change in its composition for the last 2700 cal BP. I also found that monodominant *Gilbertiodendron* forest has persisted during this time period mainly under the absence of burning which supports the hypothesis of long term minimal burning disturbance being a key factor for monodominant forest persistence. At the biome level, my results show that the relationship between climate and African rainforest has partially shifted over the last 6000 years, thus opposing the idea of climatic niche conservatism of this biome in the African continent.

This thesis provides new information of the past ecological responses of African rainforest to major environmental disturbances. African rainforests represent a globally important and largely understudied forest region, and my thesis offers fundamental insights into its ecology and biogeography.

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Contents

CHAPTER 1: INTRODUCTION

Tropical rainforest degradation has been a major concern for the last few decades. This has led to increased international research focus on this globally important biome. There are now many research efforts to understand better its diversity, ecology, ecosystem functioning, and provisioning of ecosystem services. Together with the need to identify the factors that have led to historic degradation, however, it is pertinent to understand rainforest persistence and resilience in the face of environmental perturbations. The number of studies that have focused on resilience of tropical rainforest to disturbances is more limited, for a large part because this requires long-term data, spanning multiple generations of rainforest trees, which are difficult to obtain. The overarching focus of this thesis, therefore, is to reduce this important data gap and to reconstruct long-term ecological records from the tropical rainforest biome, in an attempt to understand the factors that influence current rainforest composition, its drivers of change, and the resilience of different forest types to disturbance dynamics.

Among the world's tropical rainforests, the African rainforest block remains the most understudied in terms of its ecology (Malhi *et al.* 2013), paleoecology (Cole, Bhagwat & Willis 2014) and paleofires (Power *et al.* 2010). Despite the low plant diversity of the African rainforest in comparison to the Neotropical and Tropical Asian forest (Primack & Corlett 2005), more than 80% of its plant species are endemic (White 2001a). Another key characteristic of the African rainforest is the occurrence of areas of monodominant forest, which cover a larger area than in any other tropical rainforest (Primack & Corlett 2005).

Presently anthropogenic activities in the African rainforest are increasing rapidly and expansion of subsistence agriculture and the extraction of timber products are the main drivers of deforestation (Fisher 2010). In particular, slash and burning practices that are part of the agricultural expansion threaten this rainforest, mainly through the practice of clearance using fires (Bucini & Lambin 2002; Cochrane 2003). While fires as driver of change between rainforest and savannah have been extensively addressed (Lehmann *et al.* 2011; Murphy & Bowman 2012), the effect of fires, particularly those driven by human activities, within this rainforest biome and its overall effect on rainforest composition remains elusive.

Over the past few decades, the influence of a changing climate on the African rainforest has become evident in certain areas. In Ghana, for example, long-term drought in the last 20 years has led to an increase in deciduous species and a decrease in evergreen species, also causing an increase in above-ground biomass (Fauset *et al.* 2012). In contrast, in other areas such as Uganda, severe drought has led to the mortality of up to 40% of the population of certain rainforest tree species and a decrease in above-ground biomass (Lwanga 2003). Results from Lwanga (2003) have led to the hypothesis that certain parts of the African rainforest are potentially at a higher risk under future climate change than others.

Despite high uncertainties in projections of future climate change for tropical Africa (Rowell 2012) most of the African climatic models show a potential decrease in precipitation during the dry season in the west of the Congo basin (James, Washington & Rowell 2013). The effects of future climate change on the African rainforest distribution based on ecological niche models in the Congo show that this part of the rainforest will possibly be more persistent than other rainforests (Zelazowski *et al.* 2011). Ideally these simulations need to be evaluated against field observations. However, this is particularly challenging in tropical rainforests, because of the longevity of many tree species (Galbraith *et al.* 2013). It is therefore necessary to use long-term records, and in particular fossil plant and pollen records which have indeed been proven to contribute significantly to our understanding of rainforest tropical ecology resilience over time (Willis *et al.* 2013; Cole *et al.* 2014). But so far the use of palaeorecords to reconstruct the African rainforest vegetation patterns in the core area of the forest block has been limited.

Therefore, the overarching aim of this thesis is to improve our current knowledge of the likely future trajectory of the persistence of the tropical African rainforest under climate change and fire impact through reconstruction of past vegetation and burning dynamics using palaeoecological records from sedimentary sequences. Responses of these disturbances are analysed at the biome level and at the level of forest types. Specifically I seek to answer four main questions:

1. What is the role of disturbances driven by fire in determining tropical African forest types? (Chapter 2, Chapter 3 and Chapter 4).
2. Is there a difference in the response of different tropical African forest types to disturbances? (Chapter 3 and Chapter 4).
3. How much change occurred in the distribution of the tropical African rainforest in response to climatic disturbances in the last 6000 years? (Chapter 5).
4. How resilient are African forest types, and the African rainforest as a biome, to past fire and climatic disturbances? (Chapter 2, Chapter 3, Chapter 4, Chapter5).

I use a combination of palaeoecological proxies (fossil pollen, phytoliths and fossil charcoal) with spatial modelling approaches (spatial autocorrelation analysis and ecological niche models). The novelty of the work presented in this thesis is found in both the generation of new palaeoecological records from an under-studied region, and in the combination of the new data with modelling to address specific research questions around resilience of African rainforest to climate and fire disturbances. The thesis focuses mostly on the late Holocene (the last 3000 cal BP), because climate change events, increased human activities and fire activity have been reported for this period.

OVERVIEW OF THE CHAPTERS

This thesis is organized into four papers (Chapter 2 to Chapter 5) that are integrated in the final discussion (Chapter 6): In the first paper I focus on past fire regime and forest types (Chapter 2). The second and third papers focus on the responses of two specific forest types i.e. the Marantaceae forest (Chapter 3) and the monodominant *Gilbertiodendron* forest (Chapter 4), by studying their vegetation and fire history. The fourth paper provides analysis on climate change response at the biome level (Chapter 5). Below I briefly describe each of the chapters.

Chapter 2: Influence of fires in forest types. Paper 1. Influence of 1100 years of burning on the Central African Rainforest.

In this chapter I analyse fire regimes for the last 2500 cal BP after a major dry event in northern Republic of Congo. The main objective is to elucidate the possible influence of fires on the most important forest types and describe the spatial nature of fire using fossil charcoal from 12 sediment cores. The first hypothesis is that either the intensity or occurrence of fires, or both, may account for the differences seen between current forest types. The second hypothesis is that small and asynchronous fires may be an indication of human-made fires (Bennett, Simonso & Peglar 1990). The novelty of the approach is to consider not only the temporal but also the spatial component of fires.

Chapter 3: History of Marantaceae forest. Paper 2. Marantaceae and dense forest: two alternative stable states in Central Africa?

Chapter 3 focuses on Marantaceae forest, which is characterized by a sparse tree canopy and the presence of an extensive understorey of giant herbs mainly from the family Marantaceae. To better understand the relation between this forest type and fires, I compare the fossil charcoal record with a phytolith record (proxy to identify the presence of Marantaceae species) from two sediment cores collected in two current Marantaceae forests that were identified when undertaking the fieldwork to collect the data used in Chapter 2. I test the hypothesis that Marantaceae forest is a result of forest-fire interaction in the Sangha River region (northeast of Republic of Congo) rather than a succession from savannah to forest.

Chapter 4: History of monodominant *Gilbertiodendron* forest. Paper 3. Gilbertiodendron forest: Monodominant forest response to disturbances.

The fourth chapter is focused on the monodominant forest, whose main species is *Gilbertiodendron dewevrei*. In Africa several mechanisms have been studied to explain its presence but a main assumption is that this monodominant forest occurred under long-term low disturbance. By using fossil charcoal and fossil pollen from one sediment record collected in a site that is currently covered by monodominant *Gilbertiodendron* forest, I reconstruct the fire and vegetation history. Here I test the stability of the monodominant *Gilbertiodendron* forest presence for the last 2700 cal BP.

Chapter 5: Changes in rainforest distribution under past climate change. Paper 4. Testing rainforest niche stability: Changes in the Central African rainforest distribution in the last 6000 years.

In this chapter I present a large-scale spatial analysis of the African rainforest biome for the last 6000 cal BP. I model present forest distribution using ecological niche models (ENM) and simulate past distribution at 1000 year-step. These simulations are evaluated against fossil pollen records that have been previously analysed using the biomization method to describe the most likely biome through time. With these datasets I test rainforest climatic niche stability by analysing the performance of the simulations of past rainforest distribution.

Chapter 6: General discussion and main conclusions.

This chapter synthesises the main findings of chapters 2 to 5.

Finally Appendix 2 shows a review of African vegetation responses to past climate change using selected palaeorecords from the literature and this information is mentioned during this introductory chapter (Chapter 1).

The remainder of this chapter (Chapter 1) provides an introductory overview of 1) Current flora and climate of tropical African rainforest, 2) The current state of knowledge about African rainforest with regard to past climate change, paleofires and human presence, and 3) the current state of knowledge on the resilience of African rainforest.

STUDY AREA: CURRENT FLORA AND CLIMATE

The Central African rainforest is the second largest block of rainforest on earth covering approximately 2.8 million km^2 (White 2001a; Primack & Corlett 2005) and accounting for 25% of the total forest carbon stock of the world (Saatchi *et al.* 2011). In this thesis, the term "rainforest" is defined as the humid forest (semi-deciduous and evergreen) of the Guineo-Congolian ecoregion of West and Central Africa (White 1983), which is in line with other studies (Malhi *et al.* 2013; Hély, Lézine & APD contributors 2014) (Figure 1). This ecoregion has two domains, the Congo domain that expands from eastern Nigeria to Angola and the Guinea domain that covers the northern coast of the Gulf of Guinea from Gambia to Central Nigeria (Brenan 1978). I focus on the rainforest located west to 27°E, excluding the east African montane complex which experiences a different climatic regime.

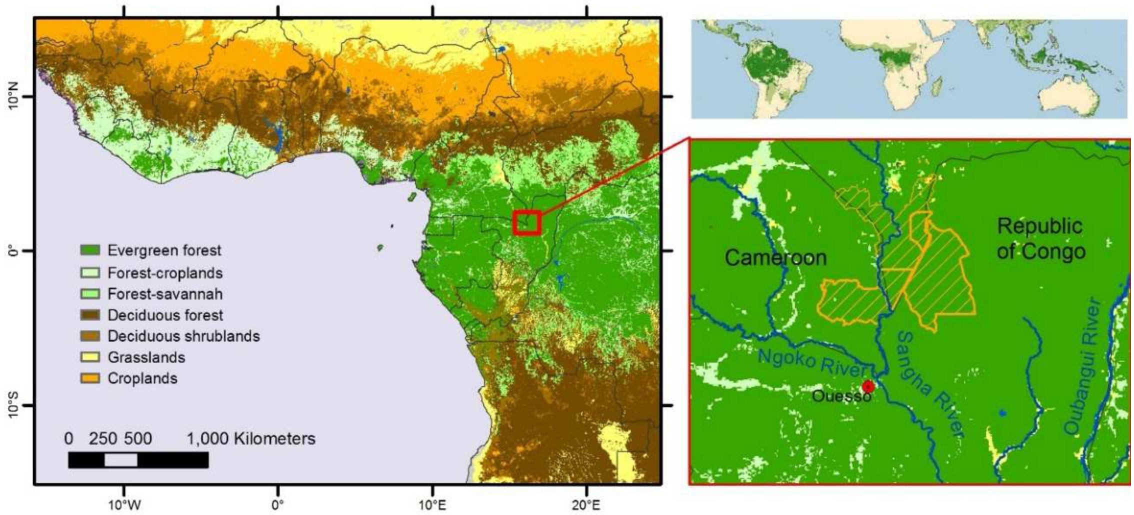


Figure 1 Study area. Left: Tropical African rainforests west to 27°E (evergreen forest in Mayaux et al. 2004). Bottom right: Location of the study area in the Sangha River region.

In comparison to other tropical regions, this is a relatively dry forest receiving between 1,600 and 2000 mm of precipitation per year in most of its extent. A coastal evergreen forest also exists with precipitation between 2,000-3000 mm (White 2001a). The general low precipitation makes African tropical rainforest more seasonal and drier than any other tropical rainforest (Primack & Corlett 2005). The abundance of the main families of plants is also different than other tropical rainforests. African rainforests are particularly poor in palms, orchids and Lauraceae, but rich in the families Dichapetalaeae and Olacaceae (Primack & Corlett 2005). In terms of structure, African rainforest has been characterized as tall stature with high above ground biomass, low stem density and high woody mass density (Lewis *et al.* 2013).

The research presented in this thesis focuses mainly on forest types (Chapter 2, Chapter 3, Chapter 4) from the Sangha River region in northern Republic of Congo (Figure 1). In this region, the main forest types identified are the mixed species *terra firma* forest (hereafter referred to as mixed forest), Marantaceae forest (sensu Gillet 2013), monodominant *Gilbertiodendron dewevrei* forest, and Swamp forest (Harris 2002; Gillet & Doucet 2012; Gillet 2013). Mixed forest is the dominant forest type in the study area of the Sangha River while *Gilbertiodendron* forest is found in dense patches sparsely dispersed between mixed forest (Fayolle *et al.* 2014 and see Figure 1 in Chapter 4).The current extent of Marantaceae forest is not known given the difficulty of separating its spectral reflectance from the one of degraded/human areas (Verhegghen *et al.* 2012; Fayolle *et al.* 2014). Finally, the swamp forest is limited to main water courses in the study area of the Sangha River and covers massive areas east and southeast of this region (Gond *et al.* 2013). An overall description of these forest types can be found in Chapter 2, and a more detailed description for Marantaceae forest and monodominant *Gilbertiodendron* forest can be found in Chapter 3 and 4 respectively.

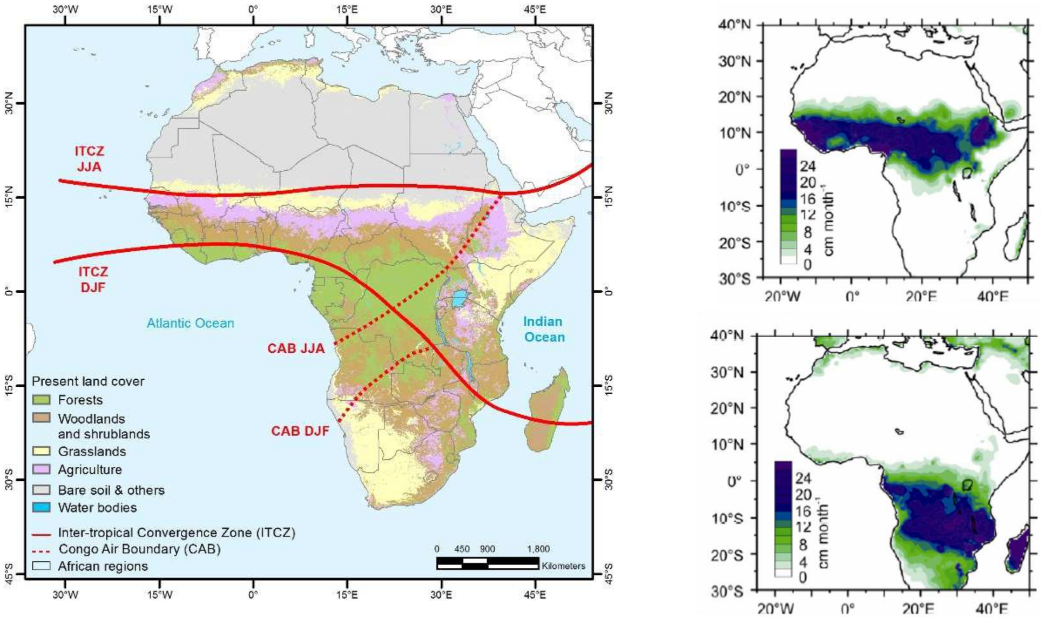


Figure 2 Climate regimes affecting the study area. Left: Approximate location of the ITCZ and the CAB in the African continent (after Willis et al. 2013) . Right: Seasonal extremes of the rain belt are shown on the right side, resp. mean precipitation for June, July and August (JJA) between 1950 and 1999 (top) and December, January and February (DJF) (from Collins et al. 2011) (bottom).

The dominant climate of the African tropical rainforest is mostly determined by the seasonal changes of latitudinal position of the Intertropical Convergence Zone (ITCZ) or Meteorological Equator, as a result of changes in insolation (maximum solar heating). The complex structure of the ITCZ and its displacement in both hemispheres leads to a variety of tropical fluxes where the two main types are the trades and the monsoon (Leroux 2001). While the trades blow from the east without crossing the geographical equator, the monsoon fluxes blow from the west and cross the equator. The nature of the monsoon complex is originally determined by a trade wind and it is no more than a vector for precipitable water, but the term “monsoon” has been used with different meanings (Leroux 2001). In recent discussion forums, the term “monsoon front” has been used to describe the rainy phase over the land (Hooghiemstra, pers. comm). This convective rainfall results from the convergence of the trade winds at the ITCZ, the Congo Air Boundary (CAB) that can be considered as a southern branch of the ITCZ, and the African Easterly Jet and Tropical Easterly Jet, with changes in insolation superimposed (Collins *et al.* 2013) (Figure 2). In and near the equator the complex system of trades and monsoon causes a bimodal pattern of rainfall with a first rainy season occurring around March and a second season occurring around November/December (Marret, Maley & Scourse 2006).

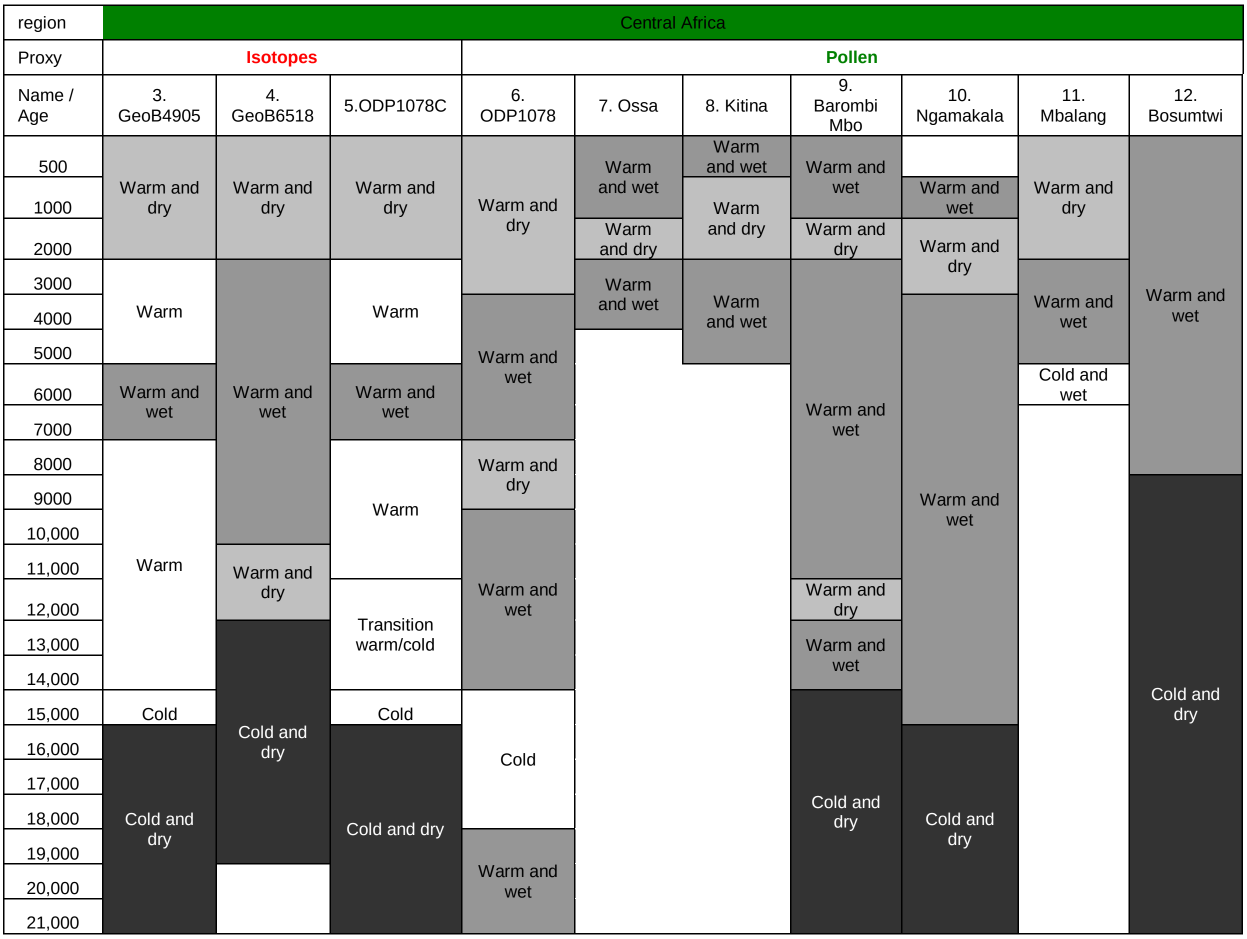
THE CENTRAL AFRICAN RAINFOREST AND ITS CHANGES DURING THE LAST 6000 YEARS

Vegetation and climate

The mid-Holocene (~ 6000 cal BP) is considered by different studies to have been the wettest period of the Holocene for Central Africa (Gasse 2000; Schefuß, Schouten & Schneider 2005). This is based on evidence from a number of different records. For example, records of deuterium/hydrogen isotopes of leaf waxes (proxy for wetness) indicate wetter conditions in Central Africa (Collins *et al.* 2013), and alkenone derived SST reconstructions (proxy for temperature) indicate regionally warmer conditions in Central Africa (Schefuß *et al.* 2005) around this interval in time relative to the present (Table 1, Figure 3). Across Central Africa, these climatic proxies (isotopes) are in agreement with vegetation proxies (fossil pollen records) of selected sites from the literature, which also indicate a warm and wet climate in the mid-Holocene, except for Mbalang in Cameroon (Table 1 and Figure 4). In that region, species nowadays associated with a cold and wetter climate are found for this period suggesting some local climatic differences (Vincens *et al.* 2010).

More recently, climatic proxies show a gradual decrease in wetness based on isotopes and a gradual increase in temperature based on SST reconstructions starting at ~3000 cal BP, suggesting a drier and warmer period than the mid-Holocene period (Schefuß *et al.* 2005; Weldeab *et al.* 2005; Dupont, Behling & Kim 2008; Collins *et al.* 2013) (Table 1). Additionally, a study using diatoms from Lake Ossa in Cameroon also supports the idea of a drier climate at around 2500-3000 cal BP. During dry conditions, Northern trade winds may bring Saharan dust to southern latitudes that contains wind-blown diatoms from Saharan Quaternary deposits. Therefore the abrupt appearance and persistence of wind-blown diatoms in Lake Ossa after 2700 cal BP is taken to suggest a marked dry period at around this time (Nguetsop, Servant-Vildary & Servant 2004).

Table 1 Temperature and wetness phases in the area covered by tropical rainforests over the past 21,000 cal BP, based on palaeo-proxies. Information of location for each record and the proxies used is detailed in Figure 3 following the number attached to each site name (from Willis et al. 2013, Appendix 2)



region	Central Africa									
Proxy	**Isotopes**			**Pollen**						
Name / Age	3. GeoB4905	4. GeoB6518	5.ODP1078C	6. ODP1078	7. Ossa	8. Kitina	9. Barombi Mbo	10. Ngamakala	11. Mbalang	12. Bosumtwi
500	Warm and dry	Warm and dry	Warm and dry	Warm and dry	Warm and wet	Warm and wet	Warm and wet		Warm and dry	Warm and wet
1000						Warm and dry		Warm and wet		
2000					Warm and dry		Warm and dry	Warm and dry		
3000	Warm	Warm and wet	Warm		Warm and wet	Warm and wet	Warm and wet		Warm and wet	
4000				Warm and wet				Warm and wet		
5000										
6000	Warm and wet		Warm and wet						Cold and wet	
7000										
8000	Warm		Warm	Warm and dry						
9000										Cold and dry
10,000				Warm and wet						
11,000		Warm and dry								
12,000			Transition warm/cold				Warm and dry			
13,000		Cold and dry					Warm and wet			
14,000										
15,000	Cold		Cold	Cold			Cold and dry			
16,000	Cold and dry		Cold and dry					Cold and dry		
17,000										
18,000										
19,000				Warm and wet						
20,000										
21,000										

Climatic proxies and vegetation proxies of the selected sites presented in Table 1 show less agreement for the last 3000 cal BP, demonstrating a higher variability in vegetation responses. Around 3000 cal BP both proxies agree on drier and warmer conditions but most pollen records shown in Table 1 show a change towards wetter and warmer conditions at different moments after 3000 cal BP. It is possible that differences in resolution are partly responsible for the disagreement because the climatic proxies have lower time resolution than the pollen records.

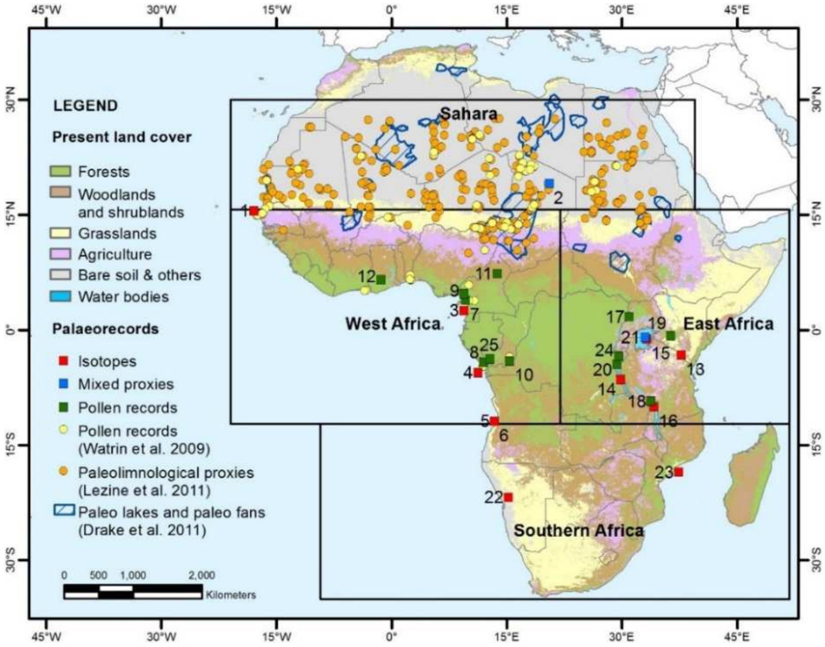


Figure 3 Location of the main palaeo-records in Africa (from Willis et al. 2013, Appendix 2)

Figure 4 shows more details on the rainforest responses to the dry event that occurred at around 3000 cal BP, including all pollen records available in the literature for this period. Pollen records across Central and West Africa show a major decrease in taxa typical of evergreen forest between 3000 and 2500 cal BP (e.g. Elenga *et al.* 1996; Reynaud-Farrera, Maley & Wirrmann 1996; Maley & Brenac 1998; Vincens *et al.* 1999; Brncic *et al.* 2007, 2009; Ngomanda *et al.* 2007, 2009b). However, conspicuous differences in species composition exist between the sites because of the disturbance caused by the climatic event. For example, a change from rainforest to savannah is observed in pollen records from west Gabon, south Congo, north Cameroon and littoral Benin during this dry event (see Figure 4 for location and Table 2 for references). These sites have not recovered their forest coverage and have remained savannahs until present time. Less dramatic changes in vegetation have been recorded in south Nigeria, southeast Cameroon, west Gabon and three other sites in the Republic of Congo. In these regions, pollen records show an increase of Poaceae and pioneer taxa during the dry event but no change to savannah has occurred (see Figure 4 for location and Table 2 for references). Only Lake Bosumtwi in Ghana shows a forest persistence without major change in its composition. These reconstructions indicate that the contraction of forest, and its conversion into savannah was not uniform across Central Africa. However, the mechanisms behind the variation across space in past rainforest responses to climate change remain little understood.

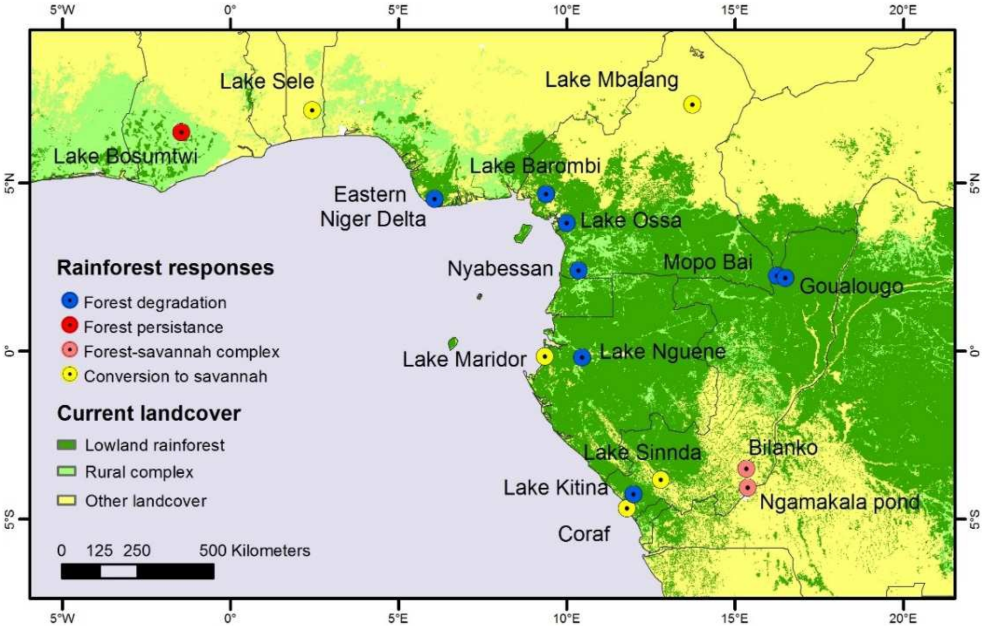


Figure 4 Rainforest responses to the dry event that occurred between ~3000-2500 cal BP. This figure shows all pollen records collected from the literature that had rainforest cover before the dry event. References are shown in Table 2.

Table 2 References for Figure 4.

Site	Country	Reference
Lake Bosumtwi	Ghana	(Maley 1991; Miller & Gosling 2014)
Lake Séle	Benin	(Salzmann & Hoelzmann 2005)
Eastern Niger Delta	Nigeria	(Sowunmi 1981)
Lake Barombi	Cameroon	(Maley & Brenac 1998)
Lake Ossa	Cameroon	(Reynaud-Farrera *et al.* 1996)
Nyabessan	Cameroon	(Ngomanda *et al.* 2009b)
Lake Mbalang	Cameroon	(Vincens *et al.* 2010)

Lake Nguene	Gabon	(Ngomanda *et al.* 2009a)
Lake Maridor	Gabon	(Ngomanda *et al.* 2009a)
Goualougo	Congo	(Brncic *et al.* 2007)
Mopo Bai	Congo	(Brncic *et al.* 2009)
Lake Sinnda	Congo	(Vincens *et al.* 1998)
Lake Kitina	Congo	(Elenga *et al.* 1996)
Coraf	Congo	(Elenga 1992)
Ngamakala pond	Congo	(Elenga, Schwartz & Vincens 1994)
Bilanko	Congo	(Elenga 1992)

Paleofires during the last 6000 cal BP

Only a limited number of studies exist that address the question of past fires in the Central African rainforest. Most of these use charcoal fragments found in soil profiles or charcoal particles extracted from sedimentary sequences as proxy for fires (Table 3). Charcoal fragments collected in soil profiles can be dated indicating the approximate time of burning, but frequently this dating is absent and only the depth at which the fragment was collected is recorded. Given the different methods of quantifying the charcoal in the different studies, it is difficult to compare these records. For example, in Southern Cameroon (van Gemerden *et al.* 2003) and Ituri in Democratic Republic of Congo (Hart *et al.* 1996) there are qualitative descriptions of extensive layers of charcoal under the soil but it remains unclear how these descriptions relate to the 4000 to 8000 particles of charcoal /cm^3 found by Brncic *et al.* (2007) in lake sedimentary records. While a comparison of fire intensity between records is difficult, the inference of presence/absence of fire allows to draw conclusions. For example, although two publications show absence of fire in their study sites (Giresse, Maley & Brenac 1994; Ngomanda *et al.* 2009b), most of the studies listed in Table 3 show the presence of charcoal at different periods for the last 4000 cal BP, and, therefore this is taken to indicate fire presence within the Central Africa rainforest during this period.

In addition to understanding fire dynamics by themselves, it is important to understand the relation between fires and vegetation. Two of the studies that collected charcoal fragments from soil profiles use anthracology to identify species taxa from the charcoal fragments, allowing insight in potential changes of composition due to fire disturbances. The advantage of this technique is that it identifies the truly local vegetation present at the study site in comparison to pollen. For example, pollen may also represent species that are not present at the study site but have reached the site due to their large pollen dispersal capabilities (Hubau *et al.* 2012). Using an anthracological approach, Hart *et al.* (1996) show that the rainforest of Ituri in the northeast of the Democratic Republic of Congo, has persisted for the last 4000 years with hardly any change in the dominant species. Nevertheless, some of the species that were burnt are not currently present in the forest. This shows that individualistic responses to fire disturbances and possibly climatic disturbances may be driving species composition (Hart *et al.* 1996). Another study conducted in the Luki Reserve in west Democratic Republic of Congo, also found evidence of fires in the last 2500 years, but in addition, long periods (>1000 years) with absence of fires (Hubau *et al.* 2013). This study shows that mature forest was burned at around 2300-1870 cal BP where 13 out of the 15 identified species are key species of evergreen forest such as *Gilbertiodendron* species, and suggests a resilient forest to the climatic disturbance of around 3000 cal BP.

Fossil charcoal from sedimentary sequences provides a more continuous record of fires than sub-soil charcoal, and together with pollen or phytolith analysis allows also the reconstruction of fire-vegetation dynamics. However, currently little information of this type exists for the Central African rainforest (Power *et al.* 2010). The few existing charcoal records in Central African rainforests from sedimentary sequences are three records located in Gabon and Northern Congo from which microscopic charcoal particles have been analysed (Brncic *et al.* 2007, 2009; Giresse *et al.* 2009). Different studies have demonstrated that microscopic charcoal particles (< ~150µm) extracted from sedimentary sequences represent regional fires, while macroscopic charcoal particles (> ~150µm) represent local fires occurring within a few kilometres of the collection site (Clark 1988; Carcaillet *et al.* 2001; Lynch, Clarck & Stocks 2004). Recently results of macroscopic fossil charcoal analysis from 12 sediment records collected in northern Congo have become available (Tovar *et al.* 2014, Chapter 2); these results will be discussed in Chapter 2.

Table 1 Indicators of paleofire for Central Africa.

Location	Fire indicator	Amount	Reference
Bibindi–Akom II–Lolodorf region (Cameroon)	Charcoal in soil pits	Charcoal present in 29% of the 104 samples between 4 and 120 cm depth	(van Gemerden *et al.* 2003)
Taï National Park (Cote d'Ivoire)	Charcoal in soil pits	15 charcoal fragments were dated between 230-6290 ^{14}C yr BP	(Mercader *et al.* 2007)
Ituri (Democratic Republic of Congo)	Charcoal in soil pits	Charcoal present in 70% of 416 samples (until 80cm). Charcoals were dated between 130- 4190 ^{14}C yr BP. No change in vegetation type (rainforest remained present) but change in species composition based on identification of charcoal	(Hart *et al.* 1996)
Luki Reserve (Democratic Republic of Congo)	Macro-charcoals were collected from four soil profiles	Charcoal present only for the last 2500 cal BP. Charcoal of mature forest is found at around 2050 cal BP. After, that charcoal species are those from a wooded savannah, a change that has been attributed to a climatic change to drier conditions.	(Hubau *et al.* 2013)
Okomu Forest Reserve (Nigeria)	Charcoal in soil samples	90% of the charcoal fragments were palm nut kernels. Two charcoal samples were dated between 1177-1378 AD and 1230-1300 AD. No charcoal in the first 20 cm soil depth.	(White & Oates 1999)
Lake Barombi Mbo (Cameroon)	Charcoal particles in sedimentary sequence	None charcoal in the last 25,000 cal BP	(Giresse *et al.* 1994)
Different areas in Northern Congo and Cameroon (Northern Republic of Congo and Cameroon)	Macro-charcoals were collected from nine pedoanthracological profiles	Charcoal of *Gilbertiodendron dewevrei* under a current monodominant forest of *G. dewevrei* (40 cm depth, 1421-1327 cal. BP). Charcoal of *Pterocarpus soyauxii* and *Millettia drastica* have been found under an open Marantaceae forest at 40 cm depth (1184-1055 cal. BP). Abundance of the non-pioneer light-demanding species *P. soyauxii* decreased over time (levels 20 to 40 cm depth) to the benefit of giant herbs.	(Morin-Rivat *et al.* 2012)
Lake Kamalété (Gabon)	Charcoal particles in sedimentary sequence	Abundant charcoal along the section of the core corresponding to 500-1250 cal BP	(Giresse *et al.* 2009)
Goualougo in Nouabale´-Ndoki National Park (Republic of Congo)	Microscopic charcoal in sedimentary sequence	Largest peak of 8000 particles/cm3 between 100 and 200 cal BP and smaller peaks of 2000 particles/cm3 between 1750 and 2000 cal. BP; and around 2750 cal. BP	(Brncic *et al.* 2007)
Mopo Bai near to Shangha River (Republic of Congo)	Microscopic charcoal in sedimentary sequence	Three peaks of +-4000 particles/cm^3 between 0 and 900 cal BP	(Brncic *et al.* 2009)
Nyabessan (Cameroon)	Microscopic and macroscopic charcoal in sedimentary sequence	None charcoal particles found for the period 3100-2300 cal BP	(Ngomanda *et al.* 2009b)

The fossil charcoal data from the two lake sedimentary sequences collected in northern Congo (Brncic *et al.* 2007, 2009) provides the best data to describe fires chronologically, as well as changes in their intensity and relation with vegetation. Unfortunately this is limited to the Sangha River region. These records give evidence of constant regional fires in the past (microscopic charcoal) for the last 3000 years, with a marked increase in the last thousand years and with the strongest signal in the last 600 cal BP (Brncic *et al.* 2007, 2009). These fires have been associated with an increase in pioneers and light demanders. In addition to the relation fire-vegetation these studies also discuss the nature of fires. Brncic *et al.* suggest that fires were human-induced, and that they occur in association with the development of shifting cultivation. This hypothesis is supported by evidence that wetter conditions prevailed after 700 cal BP, which should lead to forest recovery. In other areas of Central Africa, a recovery of forest trees in the last thousand years is indeed observed (Vincens *et al.* 1999). Such recovery is not, however, recorded in the palaeoecological records analysed by Brncic and colleagues, which show a high abundance of both pioneer taxa and charcoal.

Overall, a large gap still exists in charcoal data collection, which inhibits a full understanding of fire dynamics in the rainforest for the African region and its relation with vegetation.

Human presence in the African tropical rainforest during the late Holocene

Although people are known to have been present in the area currently covered by African rainforest in the Congo basin, data based on archaeological sites suggests that human presence in the area was limited and sparse before 3800 cal BP (Oslisly *et al.* 2013) (Figure 5). The increased presence of humans in the rainforest during the last three millennia has been attributed to a migration process of Bantu-speaking people from the Nigeria-Cameroon border southwards and eastwards. Today they are also present south of the current distribution of the rainforest. A number of different lines of evidence from linguistic and genetic analysis have shown that this may have occurred around 5000-3000 cal BP (Holden 2002; Berniell-Lee *et al.* 2009). Two different migratory waves have been described (Oslisly *et al.* 2013). It is believed that the first migratory wave started at around 3400 cal BP. These people may have used the string of savannahs along the Atlantic Coast of Equatorial Guinea and Gabon as a corridor to reach the mouth of the Congo River and may have been the first in using pottery. The second migratory wave may have started at 2900- 2600 cal BP in the inner part of the current rainforest, southern Cameroon, where evidence for the use of iron smelting was found. It is during these two migratory waves that agriculture appears to be introduced into the region currently covered by rainforest. This allowed a subsistence economy that combined hunting and gathering activities with farming (Neumann *et al.* 2012a).

A recent study has described in more detailed the second migratory wave at around 2800 cal BP, suggesting that the Sangha River interval was the passage used by Bantu-speaking people to colonize areas further south, taking advantage of the extensive waterways network present in the region (Bostoen *et al.* 2015). However more studies in archaeological sites within this region are needed in order to test this hypothesis (Oslisly *et al.* 2013; Bostoen *et al.* 2015).

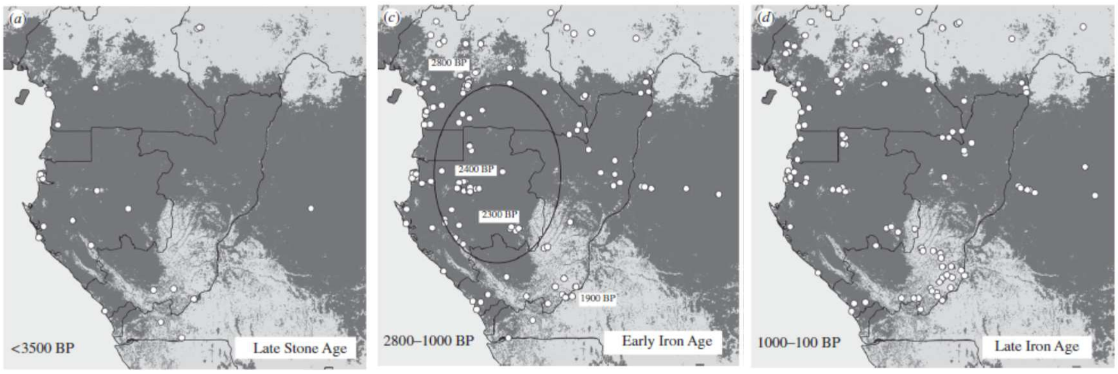


Figure 5 Archaeological sites recorded for Central Africa for different periods. Dark grey indicates areas currently covered by rainforest (from Oslisly et al. 2013)

After the second migratory wave, human population rapidly spread, particularly in Gabon and Congo (Figure 5) though population densities have fluctuated strongly. The highest peak of the human settlement in the rainforest as recorded through pottery and metallurgy, is recorded at around 1950 cal BP (Figure 6) (Wotzka 2006; Oslisly *et al.* 2013). Then, a sudden decrease in radiocarbon dates registered between 1200-900 cal BP suggests a population crash. Reasons for this notable decline in population are still under debate and remain speculative (Oslisly *et al.*

2013). A second peak in population density is observed again after 900 cal BP (Figure 5 and Figure 6).

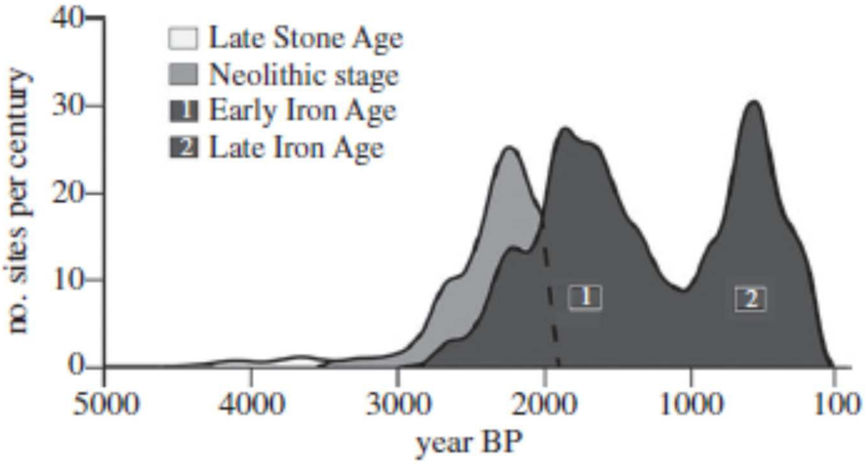


Figure 6 Radiocarbon dates (586 dates) for Atlantic Central Africa (from Oslisly et al. 2013)

Different hypotheses have linked the presence of humans, climate change and rainforest degradation. The most accepted hypothesis is that a climatic disturbance (warmer and drier conditions) at around 3000-2500 cal BP opened the forest, allowing for the presence of more people in a less hostile environment than closed rainforest and created suitable conditions for farming (Maley 2002; Neumann *et al.* 2012a). This climatic hypothesis is supported by a number of records, including fossil pollen, diatoms and archaeological evidence but has been challenged recently by a study that suggests that rather than climate, it was Bantu migration and the associated settlement at around 2500 cal BP that resulted in a major opening of the forest (Bayon *et al.* 2012). Based on an atypical high ratio of aluminium-potassium in a sediment core collected in the mouth of the Congo River, Bayon and colleagues, suggest an extensive clearance of the forest of Congo basin occurred due to human land use. However, this suggestion has been subject to criticism and several counter-arguments have been published in response. The strongest argument is that well established archaeological data supports a major signal for human settlements in the rainforest since 2000 cal BP, but not in 2500 cal BP as suggested by Bayon *et al.* (Maley *et al.* 2012; Neumann *et al.* 2012b). Hence more data are required to corroborate Bayon's hypothesis. Similar to climatic and fire proxies, archaeological data also suffer from a notable under-sampling in the African rainforests.

RESILIENCE OF AFRICAN RAINFOREST

Following Scheffer (2009), in this thesis I refer to resilience as the capacity of the rainforest/forest type to absorb disturbances and re-organize in the face of the change to mainly retain similar structure and functioning. A number of different studies have recently suggested that the tropical African rainforests are more resilient than other tropical rainforests (Fauset *et al.* 2012; Asefi-Najafabady & Saatchi 2013; Cole *et al.* 2014). These studies represent significant efforts of data collection of either field or satellite monitoring for at least ten years and meta-data studies of fossil pollen. In the long term (>100 years) resilience studies, measured as the rate at which a forest recovers following disturbance, indicate that African rainforests appear to recover faster from disturbances than South American rainforests (Cole *et al.* 2014). In the shorter term (<10 years) an analysis of canopy structure (opening of the canopy) and canopy water content over a period of strong water deficit in African rainforests show that there was hardly any significant impact, contrary to what was found in the Amazonia where significant water-stress was detected (Asefi-Najafabady & Saatchi 2013). In addition, another study that analysed the effect of 20 year drought in Ghana found that forest biomass appeared to be relatively unaffected by droughts as evidenced by an increase in biomass rather than a reduction (although in this example there was no comparison with other regions of rainforest) (Fauset *et al.* 2012).

Analysis of the different pollen records mentioned in the previous section can also contribute to infer resilience within the African rainforest. An extensive review of most of these records spanning the Holocene (11,600 cal BP) demonstrates that under a warmer and drier climate that occurred at around 3000 cal BP a variety of responses in terms of resilience can be found (Willis *et al.* 2013, Appendix 2). Some sites showed a complete conversion from forest to savannahs (low levels of resilience), while others showed medium resilience as evidenced by an opening of the canopy and increase of pioneer taxa but without conversion to savannah, while high resilient sites did not show a major change and remained as forest. Two main conclusions were deduced from this review: 1) Local factors (e.g. edaphic, geomorphic characteristics) may play an important role given the heterogeneous response observed to the same regional climatic disturbance, 2) Once a tipping point or threshold is crossed (conversion to savannah) it is difficult to recover as shown by many records that remain as savannahs until present time.

Projections of the future of African rainforest using modelling also appear to indicate inherent resilience. Results from a recent modelling study that explored future rainforest distribution demonstrated that the Congo basin may be less sensitive to climate change than the Neotropics for example, and that most of its current range will remain almost the same (Zelazowski *et al.* 2011). In addition, the projection of forest biomass carbon stocks in year 2100 that were run from a number of models all indicate a greater stock for Africa than in present time (Huntingford *et al.* 2013).

This thesis continues to address the question of resilience of the African rainforest biome (Chapter 5) but also looks at the question of the resilience of specific forest types (Chapter 3 and Chapter 4). Finally all the above mentioned studies analysed the resilience of the forest to climate change (mainly drought), however little is known about the resilience to fires. Chapter 2, Chapter 3 and Chapter 4 address this issue.

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CHAPTER 2: INFLUENCE OF 1100 YEARS OF BURNING ON THE CENTRAL AFRICAN RAINFOREST

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ABSTRACT

Four major forest types are currently present in the Central African rainforest; mixed forest, Marantaceae forest, monodominant *Gilbertiodendron* forest and swamp forest. These forest types span vast areas and demonstrate highly significant differences in diversity and productivity; yet factors responsible for their formation are poorly understood. One hypothesis is that they are as a consequence of different intensities of past human activity, in particular burning. Here we present results from fossil charcoal contained in 12 sediment cores spanning the last 2500 years and covering a spatial area of more than 900 km^2. These records demonstrate that burning started in the last 1100 years with areas currently covered by Marantaceae forest undergoing more frequent burning events than the other forest types. In comparison monodominant *Gilbertiodendron* forest appear to have undergone large burning events only in the past 200 years. These records also demonstrate a lack of spatial relationship between fire events at the different sites (discontinuous and asynchronous) suggesting that these fires resulted from localised burning events probably caused by human ignitions. Whilst the large spatial scale of past human activities in the South American rainforest is now widely acknowledged, these results indicate, for the first time, the significant impact that early human populations had on the community composition of Central African rainforest.

INTRODUCTION

It has long been recognized that Central African rainforest is far from homogeneous. Despite its low plant diversity in comparison to other tropical forests (Primack & Corlett 2005) the occurrence of endemism and the presence of distinctive forest types are high across the second largest block of rainforest of the world (2.8 million km^2) (White 2001a). In the north west of the Congo basin there are at least four major forest types recognized: 1) Mixed species terra firma forest (hereafter mixed forest), 2) Marantaceae forest with open canopy and a very dense understorey of giant herbs from the Marantaceae family, 3) Monospecific forest such as the one dominated by *Gilbertiodendron dewevrei*, a shade-tolerant species; and 4) Swamp or flooded forest (see White 1983; for a complete description Harris 2002).

A number of hypotheses have been put forward to explain the existence of these different forest types, many focusing on their relationship to various abiotic variables including climate and soils (Baker, Burslem & Swaine 2003; Blach-Overgaard *et al.* 2010). However, abiotic variables do not appear to explain the occurrence of some forest types (Peh *et al.* 2011b), or have a weak correlation (Brncic 2002). Another proposed yet little examined hypothesis is that burning events related to past human activities can explain the occurrence of these distinctive forest types. Scattered evidence for this hypothesis exists. For example, pioneer herb species such as *Megaphrynium macrostachyum* (Marantaceae) have been associated with subsoil charcoal (Brncic 2002), suggesting a possible relationship between Marantaceae forest and past fire events (Swaine 1992). In addition, the occurrence of *Gilbertiodendron* forest has been related to two opposing mechanisms: a consequence of low exogenous disturbances over long periods of time (Hart, Hart & Murphy 1989; Peh, Lewis & Lloyd 2011a) or large-scale disturbance events (Lovett *et al.* 2007) such as fires.

Three characteristics are necessary to start a fire: an ignition event, availability of flammable fuel and appropriate weather conditions (Archibald *et al.* 2009). Currently, there is much concern over the increased number of ignition events in the Central African rainforest as a result of human activities, particularly using fire to clear the forest for agriculture (Dwyer *et al.* 2000; Bucini & Lambin 2002). What is still poorly understood, however, is the flammability of the different forest types when ignited and whether an increased number of ignition events (be they human or climatically driven) will result in an alteration of the type of forest after the recovery.

To test the hypothesis that the current occurrence of the four predominant rainforest types in Central Africa is associated with past fire events, we undertook a region-wide study in the Sangha Region of the Republic of Congo (Fig. 1) to reconstruct past burning regimes using fossil charcoal contained in sedimentary sequences of 12 small lakes (< 0.5 km diameter). Two questions were addressed: 1) What was the temporal and spatial fire pattern over the last 2500 cal BP? 2) What role did past fire play in determining different forest types? Our approach significantly differs from previous studies both in the region-wide scope of the study and also in the provenance of fossil charcoal.

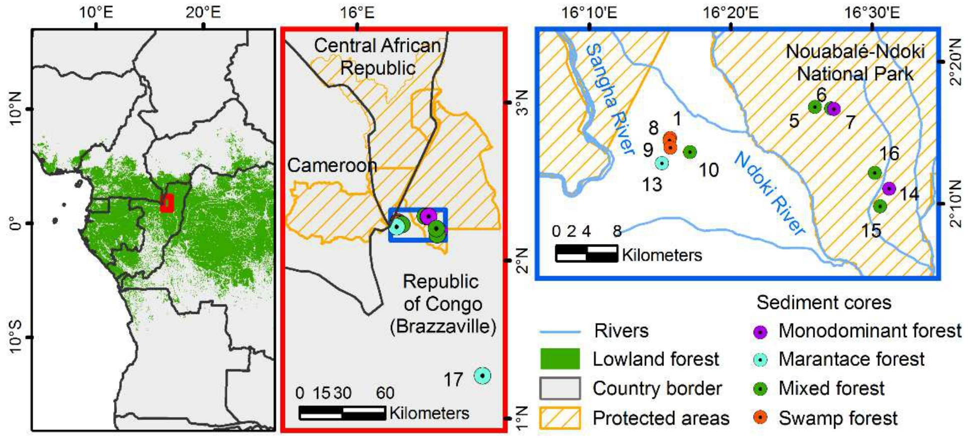

Figure 1. Study area and the distribution of the twelve core sites. Site 17 is located around 100 km south east from the rest of the cores. Sediment cores were collected in small lakes and wet forest hollows within the forest (<0.5 km in diameter, see details in Table 1).

DATA AND METHODS

Study area and description of core sites

The study area is located in the lowland forest in the northwest of the Republic of Congo (Congo Brazzaville). Across this region the total annual precipitation is approximately 1600 - 1700 mm/yr (Hijmans *et al*. 2005) with the major dry season occurring from December to February (<50 mm of rain per month) and the major wet season from September to October (Harris 2002). The elevation ranges from 330 to 490 m a.s.l.

Four major forest types are found in the region:

- Mixed forest (Mixed species terra firme forest, Harris 2002): This is the most diverse and widespread forest type in the region. It occurs on *terra firma* and is composed of emergent trees (up to 50 m) and shorter trees of different heights; therefore, the canopy is not continuous at any level. The understory varies from extremely dense to very open. Lianas are abundant, while epiphytes are less common.

- Marantaceae forest (Marantaceae forest, Gillet 2013): This forest is characterized by a sparse tree canopy and an understory dominated by giant herbs principally from the family Marantaceae (arrowroot) and/or Zingiberaceae (ginger) that may exceed five meters in height. The most typical species are *Megaphrynium macrostachyum, Haumania liebrechtsiana* and *Aframomum spp.*
- *Gilbertiodendron* forest (Gilbertiodendron dewevrei forest, Harris 2002): Species diversity is lower than in mixed forest and the main characteristic is the dominant presence of the gregarious species *Gilbertiodendron dewevrei*. The canopy is more or less continuous composed of trees reaching between 30-45 m. Low woody dwarf shrubs are common, the herb layer is almost absent, and there is a high density of lianas greater than 10 cm diameter.
- Swamp forest (Open swamp forest, Harris 2002): Forest with permanent surface water. Trees are of medium height (c. 20 m) with no continuous canopy. Small trees are less common than in mixed forest but epiphyte density is higher than in mixed forest, while large woody lianas are almost absent.

Eleven sediment cores were collected at different sites around Ndoki River, near Bomassa spanning more than 900 km^2 (Fig. 1). A twelfth sediment core was collected near Pokola (site 17), 100 km southeast from the rest of the cores. The cores were collected from water bodies that varied between seasonally flooded swampy depressions (Bais), small lake basins (Yangas) and small wet hollows in the forest; with a range between 10 and 500 m diameter (Table 1) and no inflowing stream.

Forest types for each core site were defined based on both available classification of satellite images (Devos *et al.* 2008) and vegetation description of the site during core collection. We calculated the percentage of different forest classes from the classification using a buffer of 200 m around each core site to evaluate closed vs. open canopy (see Supplementary material Appendix 1, Fig. A1).

Table 1. Details for each site and sediment core.

Id site	Forest type	Location	Site type	Basin size (Diameter in m)	Core length (cm)	Number charcoal samples	Approx. temporal resolution (yr) of charcoal sampling
Site01	Swamp forest	Mopo Bai. 2.2437° N, 16.2619° E	Seasonally flooded swampy depression (Bai)	1000 x 600	103	46	48
Site05	Mixed forest	Mbeli river. 2.2802° N, 16.4329° E	small pools, separated from the stream by a raised area	15 x 15	46	23	109
Site06	Mixed forest	Mbeli river. 2.2788° N, 16.4519° E	small pools, separated from the stream by a raised area	10 x 10	43	21	119
Site07	Gilbertiodendron forest	Mbeli river. 2.2780° N, 16.4552° E	small pools, separated from the stream by a raised area	14 x 14	59	27	93
Site08	Swamp forest	Mopo Bai. 2.2412° N, 16.2613° E	Isolated depression in a seasonally flooded swampy depression (Bai)	10 x 10	27	13	192
Site09	Swamp forest	Mopo Bai. 2.2325° N, 16.2624° E	Seasonally flooded swampy depression (Bai)	1000 x 600	101	39	64
Site10	Mixed forest	Mopo bridge. 2.2272° N, 16.2855° E	Small lake basin (Yanga)	100 x 150	71	34	74
Site 13	Marantaceae forest	Mopo bridge. 2.2141° N, 16.2524° E	Small lake basin (Yanga)	35 x 50	67	32	78
Site14	Gilbertiodendron forest	Goualougo. 2.1843° N, 16.5204° E	Small moist depression in the middle of the forest	20 x 20	86	37	68
Site15	Mixed forest	Goualougo. 2.1637° N, 16.5096° E	Small lake basin (Yanga)	100 x 100	59	33	76
Site16	Mixed forest	Goualougo. 2.2028° N, 16.5036° E	Small lake basin (Yanga)	40 x 40	33	16	156
Site17	Marantaceae forest	Pokola. 1.2708° N, 16.7970° E	Small lake basin (Yanga)	150 x 150	77	36	69

Accordingly, five of these sedimentary cores were taken in mixed forest, three in swamp forest, two in Marantaceae forest and two in the monodominant *Gilbertiodendron dewevrei* forest. Distance from the core to the nearest different forest type was also calculated (Supplementary material Appendix 1, Table A1).

Age model

The dating of the cores was carried out at the Oxford Laboratory of Luminescence using optically stimulated luminescence dating (OSL) (see Supplementary material Appendix 2, Table A2, Fig. A2 for detailed information on this procedure). We also undertook radiocarbon dating (^{14}C dates) (Poznan´ Radiocarbon Laboratory, Poland) and ^{210}Pb dating (Ortec Coaxial Well Photon Detector in the Oxford Long-term Ecology Laboratory). An age-depth model was used to establish a continuous chronology for each core. This was accomplished using the software CLAM (Blaauw 2010), fitting smooth spline models for all cores (Supplementary material Appendix 3). This model was chosen because it gave the best fit for the known dates and matches a smooth accumulation process in this area of African forest from which no dramatic changes in sedimentation were recorded.

Charcoal analysis

Fire events in Central Africa for the late Holocene have previously been studied mostly from soil profiles (e.g. Giresse *et al.* 1994, 2009; White & Oates 1999; van Gemerden *et al.* 2003; Mercader *et al.* 2007), however these studies tend to be coarse in spatial and temporal resolution and often with discontinuities in the temporal sequences. Lake sediment cores can provide a better temporal resolution and more continuous information but to date there are few studies that use fossil charcoal from lake sediment cores to examine fire dynamics over time in Central Africa (Power *et al.* 2010).

Here we used macroscopic fossil charcoal, represented by particles to be equal to or larger than 150 µm from sediment cores as a proxy for the reconstruction of local fires (Clark 1988; Whitlock & Millspaugh 1996; Carcaillet *et al.* 2001; Duffin, Gillson & Willis 2008). Previous work has demonstrated that these macrocharcoal particles are mostly deposited within 1 km of a fire (Peters & Higuera 2007; Duffin *et al.* 2008) or even within 100 m (Lynch *et al.* 2004). Most of our core sites are located more than 1 km from the nearest different forest type (Table A1), therefore, the charcoal source area is within the current forest type assigned for each site. However it is possible that a certain level of mixing exist between charcoal from cores collected in Mixed forest and *Gilbertiodendron* forest (Table A1).

Other studies in boreal and temperate forests have indicated that further dispersal of charcoal can occur (Whitlock & Millspaugh 1996; Tinner *et al.* 2006; Peters & Higuera 2007), but this is of less concern in tropical forests because here fires tend to be slow-spreading and of low intensity due to high humidity and absence of high winds (Cochrane 2003). It is therefore probable that that long-distance charcoal particle transport in tropical forest is less than in the previously mentioned ecosystems (McMichael, Correa-Metrio & Bush 2012).

For the charcoal analysis, 1 cm^3 samples were taken at 2 cm intervals across each sediment core. Each sample was mixed with 6 ml of Na hexametaphosphate (10%) and 15 ml of distilled water and left to disaggregate for 24 hours. Samples were then sieved using a mesh size of 150 µm with distilled water to collect macroscopic charcoal. Finally the macroscopic charcoal was counted on a Nikon stereoscope at 18x magnification. The influx of charcoal (particles/cm^2/yr) was calculated by standardizing the number of particles by the sediment accumulation rate of each core. A total of 357 of samples were counted with an average of 30 samples per core (Table 1). For statistical comparisons between cores, charcoal influxes were summarized as average values every 200 years since this is roughly the coarsest resolution of some of the sediment cores.

Data handling

Temporal analysis

Charcoal influx was plotted against time in bins of every 200 years for each core. A zonation procedure was applied to the data in order to obtain significant thresholds in time for the charcoal influx and to define periods that have particular patterns. This process consists of clustering adjacent samples into successively larger groups using a dissimilarity matrix between pairs of samples. For this, we used the function chclust (constrained hierarchical clustering), method CONSLINK from the Rioja package in R.

Spatial analysis

We used the UTM coordinates (obtained by a handheld GPS) of each core to calculate distances between the locations of sediment cores. Our aim in measuring spatial distance between sites was to determine if core sites situated closer together have similar charcoal influx values thus implying spatial dependency in the charcoal data. Site 17 was not included in any spatial analysis since it was located further away from other cores (100 km) and thus could have caused bias in the analysis. The analysis was conducted at two levels. The first level analyses the spatial autocorrelation of fires between the 11 sites for each bin of 200 years. The Moran's I test was then applied to the log-transformed charcoal influx values to control for the skewness of the data in Arc GIS 9.3 using an inverse Euclidean distance and standardized spatial weights (divided by row sum). Z-scores and p-values associated with Moran's Index were calculated to assess if charcoal values were clustered, overdispersed or randomly distributed over space with the assumption that fires occurring smoothly in space would indicate a regional event while random occurrence would be an indication of small isolated fires, patchy across the landscape.

In the second analysis we incorporated all the values along the time span (2500 years) to compare pairs of cores. Spearman correlation coefficient was calculated for each pair of cores using the summarized values in bins of 200 years that were previously log-transformed to reduce skewness of the data. Squared correlation values were plotted against the distance between each pair. If closer core sites have similar values of charcoal we would expect higher correlation values for smaller distances and lower correlation values for larger distances. On the contrary, a random pattern would indicate asynchrony between cores, suggesting a weak climatic control in contrast to local factors (Gavin *et al.* 2006).

Comparison between forest types

In order to explore possible relationships between forest type and fire dynamics we developed regression models to analyse fire frequency (percentage of the time series with presence of charcoal) and fire intensity (values of charcoal influx) as functions of forest types using R statistical software. Using the summarized values in bins of 200 years, fire frequency was calculated by counting the number of 200-year bins with presence of fire events with regard to the total number of bins during the last 2500 years. Presence/absence of fire was determined by transforming the charcoal influx values within each bin of 200 years into 1 and 0 values based on a threshold value. In order to account for type I error (i.e. false positive) due to e.g. long distance transport or other factors we used the median of charcoal influx values above 0 as a threshold to decide the presence or absence of a fire event. The median, equivalent to the 50th percentile, was 0.02 particles/cm^2/yr. In this way, presence of fire was registered (value 1) when bins of 200 years which have values above this threshold, otherwise a fire event was considered absent (value 0). The percentage of the time series with presence of charcoal (fire frequency) for all cores was modelled as a function of forest type using a binomial generalized linear model (GLM).

$$\text{Logit}(ch_i) = \alpha + \beta * \text{forest\_type}_i$$

where ch_i is the probability of fire event in each core, given by the percentage of fire occurrence.

After detecting overdispersion (variance in the data was larger than the mean) we controlled for this by adding an overdispersion parameter φ to the variance of the response variable. Marantaceae forest was used as a reference level for the factor forest type and significant differences between this reference level and the other forest types was assessed using a confidence level of 95%. Finally, we performed a sensibility analysis using different percentiles as thresholds to define presence/absence of fires (30th, 40th, 60th and 70th percentile corresponding to 0.01, 0.016, 0.04 and 0.09 particles/cm^2/yr respectively) to test the robustness of using the median (50th percentile) in modelling the percentage of fire occurrences.

Differences in fire intensity between forest types was assessed using a regression model where charcoal influx (summarized as average in bins of 200 years) of each core at each bin was the dependent variable and forest type and bin were explanatory variables. Preliminary analyses show the relationship between charcoal influx and bin was not linear (Supplementary material Appendix 4), and given the heterogeneity of the data per core we decided to include the cores as a random variable. Therefore, we used generalized additive mixed models (GAMM) where the variable bin was included as a smoothing function:

$$\text{charcoal}_{is} = \alpha_i + \beta * \text{forest\_type}_i + f(\text{bin}_{is}) + \varepsilon_{is}$$

where charcoal is the influx value of core i (i = core1,…,core17) in bin s (s=0,…,2400) and α_i is the random intercept (cores).

Using this model as the baseline one, other models were developed allowing heterogeneity of variances, and including different correlation structures (to account for temporal autocorrelation of each core). Finally, the different models were evaluated through their Akaike information criterion (AIC) values and we verified that the assumptions of homogeneity, normality and independence of the residuals were met. The AIC values of the different models are shown in Supplementary material Appendix 5. After selecting the most appropriate model (A: adjusted R-squared value = 0.68, and an AIC=-429.53), the ANOVA was used to test the significance of the included variables of the best model using a confidence level of 99% following the suggestion of using a more conservative confidence level when using GAMMs (Zuur *et al.* 2009).

RESULTS

Results from the cluster analysis (Supplementary material Appendix 6) indicate that the charcoal records can be divided into four distinct temporal zones (Fig. 2). In the first period, defined by cluster analysis between 2500 and 1100 cal BP almost no fires occurred at any of the 12 sites. A second period is identified between 1100-500 cal BP, showing the first occurrences of fires. During the third period, between 500-300 cal BP, both the intensity and occurrence of fires started to increase. Finally, the largest charcoal peaks occur in the last 300 cal BP. Observed peaks of influx values typically ranged from 0.05 to 0.42 particles/cm^2/yr. At site 13 (located in Marantaceae forest) the highest peaks were recorded with charcoal influx values of 3.1 particles/cm^2/yr (original charcoal influx values in Supplementary material Appendix 7, these were then summarised into 200 year bins).

In the spatial analysis, the comparison of charcoal influx values from site to site did not show any significant spatial autocorrelation ($P > 0.1$ for Moran's I index) for any 200 year bin (Supplementary material Appendix 8). The lack of spatial autocorrelation between sites suggests fires have occurred randomly in space at least at this bicentennial scale. When the whole time series of charcoal influx of each site is compared against other sites to obtain correlation values to plot against distance (see methods), there is also no clear pattern (Fig. 3). Correlation between the different time series does not decrease with increasing distances. High values of correlation are found at closer sites as well as sites separated by more than 30 km. Closer sites show both high and low correlation values. These results indicate temporal asynchrony of fire events between core sites.

When analysing fire frequency (percentage of the time series with presence of charcoal) results indicate that areas currently containing Marantaceae forest have undergone significantly more fire events in the last 2500 years than those that have monodominant *Gilbertiodendron* forest, Mixed forest and Swamp forest (Table 2). Around 40% of the time series in the two sites currently occupied by Marantaceae forest show a fire event (Fig. 4). The sensibility analysis using different thresholds than the median to decide presence or absence of fires also confirms that Marantaceae forest has more frequent fire events than other forest types (Table 2, Supplementary material Appendix 9). Thus areas with Marantaceae forest show that there were fires in every 200- year bins for the last 800 years (Fig. 2). In contrast, the areas currently occupied by monodominant *Gilbertiodendron* forest appear to have only small episodes of fire before 600 cal BP and then a large charcoal peak is registered in the bin of the last 200 years (Fig. 2).

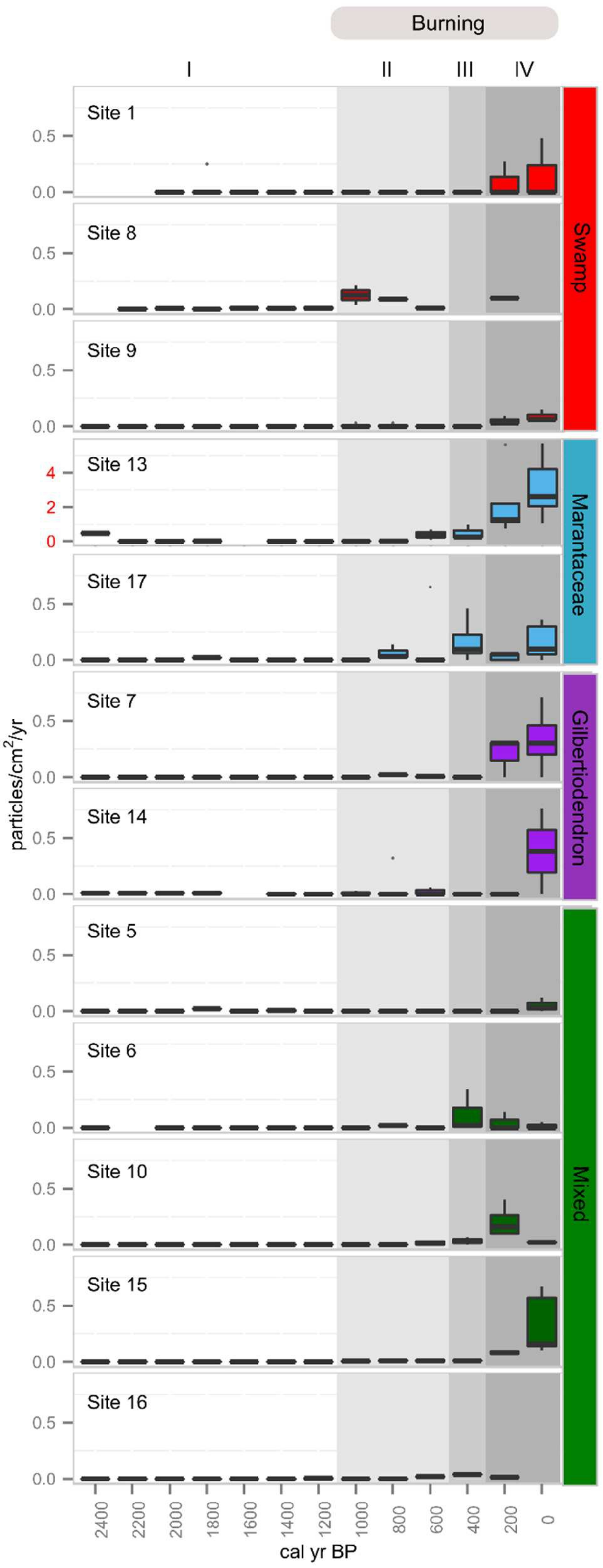

Figure 2. Boxplots of charcoal influx values summarized every 200 years for each core for the last 2500 cal BP (particles/cm^2/yr). Four periods are identified: I) Minimal fires (2500-1100 cal BP), II) First occurrences of fires (1100-500 cal BP), III) Increasing fires (500-300 cal BP), IV) Highest peaks of charcoal (300-0 cal BP). Site 13 is shown at a different scale.

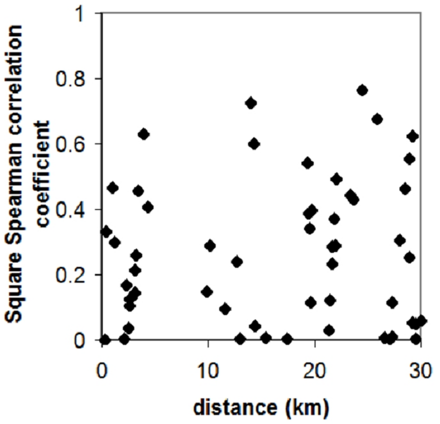

Figure 3. Correlation between charcoal influx values of paired cores against the Euclidean distance of each pair of core sites. No trend is observed, suggesting a random spatial pattern of fire events.

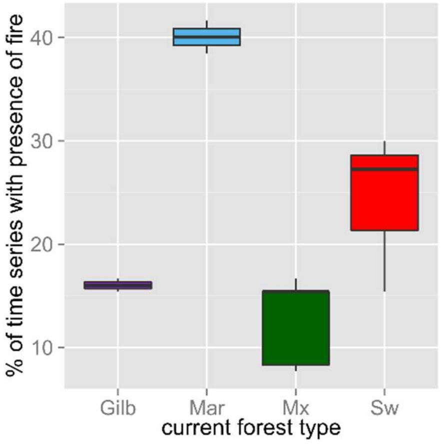

Figure 4. Boxplots showing fire frequency per forest type. The percentage is based on the number of 200 year bins with a presence of fire for the last 2500 cal BP. Fire presence is defined as equal to or above the median (50th percentile) of charcoal influx values. Differences between forest types were tested using a binomial GLM. Gilbertiodedron, Mixed and Swamp forest show statistically significant lower frequency of fires than Marantaceae forest (See text and Table 2). Other thresholds were tested as sensibility analysis (Table 2 and Supplementary material Appendix 9). Sw: samp forest, Mx: mixed forest, Mar: Marantaceae forest, Gilb: Monodominant Gilbertiodendron forest.

In comparison to frequency of fires, there appears to be no significant relationship between fire intensity (charcoal influx values) and forest type at a significance level of 99% (Table 3). This result, therefore, suggests that one particular forest type does not burn more than another. However, there is a significant negative non-linear relationship between charcoal influx and time

(Table 3, Supplementary material Appendix 10); which indicates a trend at all sites with respect to time, with more burning occurring in recent years.

Table 2. Summary of the binomial GLM of fire frequency (percentage of time series with presence of fire) against forest type. The level Marantaceae forest was used as the reference one for the factor forest type. Table shows the results for different thresholds used to define the presence or absence of fires (30th, 40th, 50th, 60th, 70th percentiles of charcoal influx values).

Percentile	Variables	Estimate	Std. Error	t value	Pr(>|t|)	Signif.
30th	(Intercept)	-0.2615	0.2419	-1.081	0.3112	
	forest type gilbertiodendron	-0.8912	0.3706	-2.405	0.0429	*
	forest type mixed	-0.9133	0.3007	-3.037	0.0161	*
	forest type swamp	-0.8912	0.3333	-2.674	0.0282	*
40th	(Intercept)	-0.2615	0.2392	-1.093	0.30618	
	forest type gilbertiodendron	-0.8912	0.3665	-2.432	0.0411	*
	forest type mixed	-1.1	0.3031	-3.629	0.00669	**
	forest type swamp	-0.8912	0.3296	-2.704	0.02691	*
50th	(Intercept)	-0.4263	0.1922	-2.219	0.05729	.
	forest type gilbertiodendron	-1.2696	0.3229	-3.931	0.004349	**
	forest type mixed	-1.5473	0.2643	-5.854	0.000381	***
	forest type swamp	-0.7263	0.263	-2.762	0.02461	*
60th	(Intercept)	-0.5971	0.3041	-1.963	0.08522	.
	forest type gilbertiodendron	-1.4435	0.5483	-2.633	0.03005	*
	forest type mixed	-1.7165	0.4427	-3.878	0.00469	**
	forest type swamp	-0.7278	0.4215	-1.727	0.12246	
70th	(Intercept)	-0.7538	0.3726	-2.023	0.07769	.
	forest type gilbertiodendron	-1.2869	0.66	-1.95	0.08703	.
	forest type mixed	-2.3248	0.6527	-3.562	0.00738	**
	forest type swamp	-1.4811	0.6078	-2.437	0.04078	*

Table 3. Results of the best GAMM model for charcoal influx against forest type and time (200-year bin).

GENERAL SUMMARY

Parametric Terms:		df	F	p-value
forest_name		3	2.773	0.0439

Approximate significance of smooth terms:	edf	Ref.df	F	p-value
s(bin)	6.438	6.438	47	<2e-16

DETAILED SUMMARY FOR PARAMETRIC TERMS

Variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.04149	0.013148	3.156	0.00197
forest type gilbertiodendron	-0.0009	0.020613	-0.044	0.96508
forest type mixed	-0.03065	0.013448	-2.279	0.02422
forest type swamp	-0.02893	0.01324	-2.185	0.03061

DISCUSSION

A number of hypotheses exist relating to the spatial distribution of diversity in forest types in Central African rainforest. These include those that attribute the influence of abiotic factors on forest type (Baker *et al.* 2003; Peh *et al.* 2011b) and those that consider biotic factors such as species traits or disturbances. Here we focus on the possible effect of disturbance through fire. We have tested for the first time the hypothesis that a potential relation between long-term fires and forest types in Central Africa may exist. This is particularly important, as currently the majority of fire events occurring worldwide in the evergreen forest biome are recorded from the African continent (Dwyer *et al.* 2000). Our results, using multi-site sediment cores spanning the last 2500 years, provide new insights of both the role of fire in shaping some forest types and the nature of ignition events.

Role of fire in shaping forest types

Our region-wide study indicates that those areas that have experienced more frequent burning in the past are currently occupied by Marantaceae forest where the dominant giant herb is *M. macrostachyum* (Fig. 4). *M. macrostachyum* grows in forest clearings, reducing light availability on the forest floor and inhibiting growth of tree seedlings through root competition for below-ground space (Brncic 2002). Several authors have suggested that Marantaceae forest is a stage within the natural succession from savanna to forest, especially in areas where savannas are adjacent to Marantaceae forest (e.g. in littoral Congo and Lopé, Gabon) (de Foresta 1990; White 2001b). However such enclosed savannas are currently absent in our study area and its surroundings (Gillet & Doucet 2012). Furthermore, there is no evidence of a savanna phase in our study area in the last 2500 cal BP (Brncic *et al.* 2007, 2009). Therefore, according to our results, the establishment of *M. macrostachyum* may be associated with frequency of fires in forest rather than savanna conversion to forest.

In contrast, the two sites that appear to have had almost no burning, followed by the occurrence of a high charcoal peak around 200 years ago, are now covered by the monodominant

Gilbertiodendron forest (Fig. 2). This provides support for the hypothesis that a major disturbance is needed to establish this forest type (Lovett *et al.* 2007). It also suggests the possibility of a parallel with the vegetation history of *Gilbertiodendron dewevrei* in the Ituri in the Democratic Republic of Congo (Hart *et al.* 1996). Hart *et al.* showed that although evergreen forest had been present for the last 4000 years from the identification of sub-soil charcoal, it appears that *Gilbertiodendron* arrived and formed mono-dominant stands very recently. The mechanisms behind the establishment of *Gilbertiodendron* remain under discussion (Peh *et al.* 2011a).

In terms of flammability our study suggests that there is little discernible difference between forest type and intensity of burning (Table 3); thus, in contrast to frequency of burning, there is no discernible relationship between amount of charcoal and forest type. However we used a conservative p-value (0.01, recommended for this type of models). At a p-value of 0.05, current areas of Marantaceae forest would have statistically significantly higher charcoal values than Mixed forest and Swamp forest but not higher than *Gilbertiodendron* forest (see table 3). More cores would be needed to test this as well as data on how the occurrence of Marantaceae species changed through time.

Here we have shown that fires play a role in determining forest type, however, other factors remain untested as potential drivers of forest type occurrence such as interaction between species.

The role of humans in shaping the fire events

Natural fires are not common in tropical rainforest due to the high humidity present in this biome (Scott 2000) and in Central Africa, natural fires have rarely been reported in modern times (e.g. Tutin, White & Mackanga-Missandzou 1996). However, drought cycles can lead to fire events in tropical rainforest (Stott 2000), as has been documented for the Amazon basin during the early and mid-Holocene (Urrego *et al.* 2013). An extended dry season occurred between 3000 and 2500 cal BP in Central West Africa (Maley 2002; Vincens *et al.* 2010; Bonnefille 2011) with some evidence to suggest that this lead to a major decrease in taxa typical of evergreen forest in some regions (Elenga *et al.* 1996; Reynaud-Farrera *et al.* 1996; Maley & Brenac 1998; Vincens *et al.*

1999; Brncic *et al.* 2007, 2009; Ngomanda *et al.* 2009b). Yet, our results do not show a high occurrence of fire events after 2500 cal BP. On the contrary, fires are minimal between 2500-1100 cal BP which may imply that either ignition events or fuel load, the other necessary components to start a fire (Archibald *et al.* 2009), were not adequate.

There is less evidence for the occurrence of a dry event in Central Africa around 1100 cal BP, when fires started in our study area, a time that coincides with the beginning of the Medieval warm period recorded for the northern hemisphere. Pollen records in Cameroon and Congo show a recovery of primary forest or forest cover after around 1000 cal BP suggesting wetter conditions (Elenga *et al.* 1994; Reynaud-Farrera *et al.* 1996; Vincens *et al.* 1998). However, high temporal resolution pollen records from Gabon suggest a fluctuation of dry/wet events around this time (Ngomanda *et al.* 2007) and species assemblages reconstructed from charred wood remains suggest a dry event occurred between 1100 and 700 cal BP in the Democratic Republic of Congo (Hubau *et al.* 2013).

Pollen records from previous studies in two of our sediment cores do not show a major change in composition at 1100 cal BP (Brncic *et al.* 2007, 2009) which may imply that climate did not change much towards a specific dry event or that dry events occurring across Central Africa were not synchronous or were localized. Also, there is no indication of a reduction in burning during the Little Ice Age when wetter conditions were observed after 600 cal BP in the region (Elenga *et al.* 1996; Brncic *et al.* 2007; Bonnefille 2011).

The lack of spatial and temporal autocorrelation between charcoal values of the different sites (spatially discontinuous and asynchronous fires) is indicative of the individual nature of the burning events. Previous work has demonstrated that random or discontinuous fire occurrence may represent isolated human-made fires (Bennett *et al.* 1990). This, combined with the low values of charcoal influx suggests fires were possibly caused by slash and burn activities. Additionally, in the late Holocene, it seems that asynchronies are not unusual between relatively close sites (Gavin *et al.* 2006; Hu *et al.* 2006; Urrego *et al.* 2013) and climate would have a weak control over fires in contrast to other local factors (Gavin *et al.* 2006) such as human activities, as we propose here.

There is extensive evidence for a regional settlement by the Bantu who migrated into this central equatorial forest around 2400-2500 cal BP (Wotzka 2006; Neumann *et al.* 2012a; Oslisly *et al.* 2013). Pollen records, diatoms and archaeological evidence propose that a climatic disturbance created more suitable livelihood conditions for migrating Bantu-speaking farming populations (Neumann *et al.* 2012a). Two marked increase points in pottery and metallurgy have been registered in rainforest (>15°E) around this time. The first one around 2000 cal BP and other after 1000 cal BP (Wotzka 2006; Oslisly *et al.* 2013). This latter peak around 1100 cal BP may be related with the beginning of fires in our study area. Indeed, around 15 km north of the study area, fragments of pottery dated by OSL to approximately 2000-600 cal BP confirm human presence in the forest (Brncic 2002). Therefore, evidence, including data from this study, suggests human influence may be responsible for the ignition events that caused the vast majority of fires that occurred in the last 1100 years in this part of the Central African rainforest.

It is possible that within the two Marantaceae forest sites, the larger values of charcoal influx found in site 13 in comparison to site 17 may be explained by a a larger human presence in site 13. Indeed, according to a recent study, soil pits near Bomassa (site 13) contain around 140 pottery shards/m^3, while soil pits in Ibamba (site 17) contain 2 shards/m^3 (Gillet 2013). Population near Bomassa has also a larger tradition of slash and burning activities while near Ibamba, hunter and gatherers are more common (Gillet 2013). Despite the large differences in charcoal influx in both sites, fire frequency patterns were similar, thus highlighting the importance of the number of human-induced fire events in this forests.

CONCLUSIONS

We have shown that, for the last 1100 years, fires in this part of the Central African rainforest have been probably mostly caused by human activity, and that these fires may have influenced the distribution of present-day forest types such as Marantaceae forest and monodominant

Gilbertiodendron dewevrei forest. Our results indicate that it is not the flammability of the different forest types but rather the number of ignition events which has varied between the fire regimes. This study is the first to point towards humans rather than climate as causing fires over this period and probably affecting forest types. Given the current increased human activity in this forest in the form of logging, road building, mining, agriculture and settlement, we may expect to see, in addition to the conversion of forest to non-forest, significant increases in some types of forest such as Marantaceae dominated forest. Future vegetation modelling of the region for different land use and climate change scenarios should take this into account.

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SUPPLEMENTARY MATERIAL

(Appendix ECOG-00697 at <www.ecography.org/readers/appendix>).

Appendix 1–10.

Appendix 1.

Vegetation description of each core

We recorded the main species present at each site where cores were collected and assigned a preliminary forest type based on this data. Swamp forest was easily identified. To further corroborate our designation of *Gilbertiodendron*, Mixed and Marantaceae forest we used available classifications of satellite images (Devos *et al.* 2008) to determine the forest surrounding the core sites using a buffer of 200 m radius. This analysis (Fig. A1) gave us percentage values of open vs closed canopy which we used to assign the forest type as follows: Swamp forest (sites 1, 8 and 9) was characterized by more than 50% of semi-open and open canopy cover and included typically swampy species. Mixed forest (sites 5, 6, 10, 15 and 16) was characterised by closed canopy cover (closed canopy and closed canopy *Gilbertiodendron*) of more than 50% but the class “closed canopy *Gilbertiodendron*” covers less than 50% of the area within the 200 m radius. In cases when at least 50% of the land cover was represented by the class “closed canopy *Gilbertiodendron*”, the core site was assigned as monodominant *Gilbertiodendron* forest (sites 7 and 14). Finally, we assigned the class Marantaceae forest to core sites with more than 50% of semi open and open canopy cover, and where the presence of patches of *Megaphrynium macrostachyum* was recorded (sites 13 and 17). Site 17 also has *Haumania liebrechtsiana*, and a more open canopy than site 13. The location and details relating to each core are shown in Table 1.

Using the same classification we calculated the distance of each site of collection to the nearest different forest type (Table A1).

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Table A1. *Distance to the nearest different forest type for each site of core collection.*

Id core	Current forest type	Nearest forest	Distance to the nearest forest at present (m)
Site 1	Swamp	Mixed	800
Site 8	Swamp	Mixed	1100
Site 9	Swamp	Mixed	1300
Site 13	Marantaceae	Swamp	2000
Site 17	Marantaceae	Swamp	1500
Site 7	*Gilbertiodendron*	Mixed	500
Site 14	*Gilbertiodendron*	Mixed	500
Site 5	Mixed	*Gilbertiodendron*	1800
Site 6	Mixed	*Gilbertiodendron*	500
Site 10	Mixed	Swamp	2500
Site 15	Mixed	*Gilbertiodendron*	2000
Site 16	Mixed	*Gilbertiodendron*	500

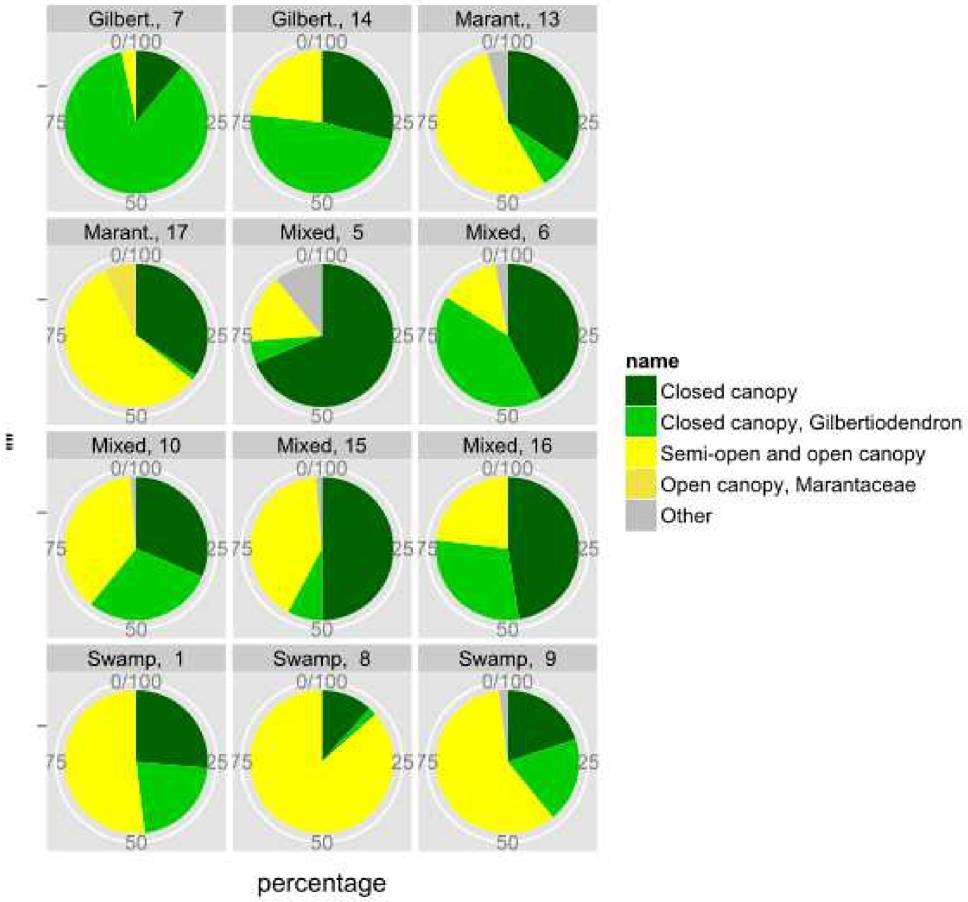

Figure A1. *Forest coverage in percentage for every site.*

Appendix 2.

Optically stimulated luminescence dating (OSL)

Luminescence methods provide estimates of the total radiation dose absorbed (D_e, units Gy) by sedimentary grains during burial. Estimation of burial age (in units ka, thousands of years) is possible if the mean radiation dose rate (D', units Gy/ka) is known, and in this case Age = D_e/D' (Aitken 1998).

Sediment samples from the sediment cores were extracted for optical dating under laboratory conditions. The exposed face of the sediment core was excavated to a depth of 20 mm under subdued amber (580 nm) lighting (demonstrated to have negligible effects on quartz OSL signals). The samples were processed under the same lighting conditions in order to extract refined quartz grains. Each sample was washed in distilled water to remove <15μm material and sieved, retaining the 180-250 μm fraction. This material was immersed for two days in 1 M HCl to remove carbonate, washed in distilled water, immersed for two days in H_2O_2 to remove organic matter, and washed again in water. Heavy minerals (density >2.72 g/cm^3) were removed from the treated sample fraction by heavy liquid (sodium polytungstate) separation. The <2.72 g/cm^3 fractions were then etched with 48% HF for 60 minutes, followed by HCl and water rinses to remove precipitates. The HF treatment removes potassium feldspar and etches the outer (alpha-irradiated) surface of the quartz grains. The remaining quartz grains were re-sieved to the original grains size range. Sub-samples of each prepared quartz sample were mounted for single grain measurement.

Optically stimulated luminescence measurements were made using an automated Risø TL/OSL DA-15 reader (Botter-Jensen *et al.* 2000), with single-grain attachment. Optical stimulation of individual quartz grains was achieved using a 10 mW Nd:YVO_4 diode pumped laser, providing approximately 50 W cm^{-2} in a focused 30 μm spot at 532 nm to each grain. IR stimulation of the sample disc was provided by diodes at 880 nm (approx. 400 mW cm^{-2}). Samples were irradiated using a calibrated ^{90}Sr/^{90}Y beta source. The ultra-violet (~370 nm) component of the emitted luminescence was measured using a photomultiplier (type 9235QA) filtered with two Corning U-340 glass filters. Equivalent doses were determined using the Single-Aliquot Regenerative-dose (SAR) procedure (Wintle and Murray 2006). Samples were preheated for 10 s at 260°C prior to measurement of natural and regenerative dose (L_x) points, and for 10 s at 220°C prior to the sensitivity correction (T_x) measurements. All OSL measurements were made at 130°C.

Grains were selected for inclusion in D_e analysis which passed the following criteria: ‘recycling ratio’ and ‘IR depletion ratio’ within 10% and/or 2σ of unity, ‘zero-dose ratio’ within 10% and/or 2σ of zero, dose response data successfully described by the fitted ‘exponential-plus-linear’ function. Fitting success was defined as the fit passing within 1σ of each L_x/T_x point. This is a rather conservative criterion but judged appropriate given the ratio of data points to fitted parameters (six regeneration points and four free parameters). The statistical uncertainties on each L_x/T_x measurement were based on counting statistics and were propagated through to an uncertainty on D_e (σD_e) using a Monte Carlo procedure (each growth curve dataset being sampled 1000 times); a further systematic uncertainty of 3% was added in quadrature to each σD_e value to account for calibration errors and machine reproducibility. Grains with relatively low sensitivity were included in the analysis but naturally contributed little to the estimate of D_e due to the weighting of individual estimates. Depending on raw sample size (sampled volume and quartz yield) and the proportion of luminescent grains, between approximately 300 and 700 grains were measured for each sample. Of these, the number of 'successful grains' (n) used for D_e estimation is given in Table A2.

For each sample, the degree of skewness in D_e values (weighted by uncertainty in each D_e estimate) was significant at 95% (Bailey and Arnold 2006). An example is shown in Figure A2 for sample Con09-10-86 (skewness=2.5; threshold for 95% significance is 0.68). Given the depositional environment and the significant degree of skewness observed, these samples are interpreted as having been heterogeneously (partially) bleached prior to deposition (see Bailey and Arnold 2006 for discussion). The Minimum Age Model (MAM) of Galbraith *et al.*(Galbraith *et al.* 1999) was used to estimate D_e (implemented using the S script circulated amongst the luminescence community by Dr Rex Galbraith) apart from in cases where no numerical solution could be found or where individual low D_e estimates produced a dominant effect resulting in dates being out of stratigraphic order. For these cases (approx. 30% of the samples), the Finite Mixture Model (e.g. Jacobs *et al.* 2008) was used to estimate D_e, taking the first component greater than the low-lying estimate. In the present case this is a suboptimal solution to the problem of estimating D_e from scattered natural dose populations with low 'outliers' but was deemed preferable to other options, such as the outright rejection of samples.

During burial, the radiation dose-rate (D') comprises contributions from β-, γ-, and cosmic-radiation (Aitken 1998). The β and γ components of D' result from the radioactive decay series of ^{238}U, ^{232}Th and from ^{40}K within the sediment. These parent isotopes were measured using

Inductively Coupled Plasma Mass-Spectrometry (ICP-MS) and their decay products were assumed to be in constant abundance throughout the burial period. The measured radionuclide concentrations were converted directly to estimates of D' (Adamiec and Aitken 1998), assuming a water content of 17±7% (water mass as a fraction of total wet sediment mass; a value of 50% saturation was chosen for dose rate calculations, defined from porosity measurements on a subset of samples, with errors conservatively estimated as 50% of the saturation value) and correcting for size-dependent β-attenuation through the quartz grains. The cosmic dose contribution to D' was calculated according to (Prescott and Hutton 1994), assuming an overburden density of 2 g/cm^3, taking in to account sampled depth, site altitude and geomagnetic latitude.

The final age uncertainty in each case includes uncertainties on D_e values (which include errors due to photon-counting statistics, curve fitting/interpolation, source calibration, machine reproducibility), all isotope concentrations, dose-rate conversion factors; attenuation/absorption factors, water content, burial depth and overburden density. A data summary is given in Table A2.

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Table A2. *Summary data for calculation of OSL ages. D_e is the 'equivalent dose' (the estimate of the total absorbed radiation dose), and n is the number of grains accepted according to the selection criteria described in the main text. All other values are as described in the main text.*

Sample ID	CON09-1-2	CON09-1-12	CON09-1-26	CON09-1-38	CON09-1-60	CON09-1-100
D_e (Gy)	0.04 ± 0.004	0.37 ± 0.05	0.81 ± 0.14	1.48 ± 0.22	1.73 ± 0.19	2.16 ± 0.1
n	135	54	65	48	111	129
Depth (m)	0.02 ± 0.01	0.12 ± 0.05	0.26 ± 0.05	0.38 ± 0.04	0.6 ± 0.05	1 ± 0.1
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210	150-210
U (ppm)	0.87 ± 0.09	0.87 ± 0.09	1.13 ± 0.11	1.15 ± 0.11	1.18 ± 0.12	1.18 ± 0.12
Th (ppm)	8.91 ± 0.89	8.68 ± 0.87	10.38 ± 1.04	10.24 ± 1.02	9.98 ± 1	10.22 ± 1.02
K (%)	0.033 ± 0.002	0.025 ± 0.001	0.025 ± 0.001	0.025 ± 0.001	0.025 ± 0.001	0.025 ± 0.001
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.2 ± 0.1	0.2 ± 0.08	0.2 ± 0.04	0.19 ± 0.02	0.19 ± 0.02	0.18 ± 0.02
Total D' (Gy/ka)	0.89 ± 0.13	0.87 ± 0.11	1.01 ± 0.1	1.01 ± 0.1	0.99 ± 0.09	0.99 ± 0.1
Age (years)	45 ± 8	424 ± 80	800 ± 160	1471 ± 260	1746 ± 253	2173 ± 233

Sample ID	CON09-5-2	CON09-5-22	CON09-6-2	CON09-6-22	CON09-6-42	CON09-6-76
D_e (Gy)	0.05 ± 0.01	0.96 ± 0.09	0.12 ± 0.13	0.41 ± 0.1	2.22 ± 0.09	4.03 ± 0.21
n	32,000	62,000	37,000	41,000	28	9,000
Depth (m)	0.02 ± 0.01	0.22 ± 0.05	0.02 ± 0.01	0.22 ± 0.05	0.42 ± 0.05	0.76 ± 0.05
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210	150-210
U (ppm)	1.13 ± 0.11	0.78 ± 0.08	1.22 ± 0.12	0.93 ± 0.09	0.96 ± 0.1	1.06 ± 0.11
Th (ppm)	6.04 ± 0.6	4.93 ± 0.49	8.97 ± 0.9	6.85 ± 0.69	7.86 ± 0.79	9.36 ± 0.94
K (%)	0.108 ± 0.005	0.075 ± 0.004	0.033 ± 0.002	0.033 ± 0.002	0.025 ± 0.001	0.017 ± 0.001
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.2 ± 0.1	0.2 ± 0.05	0.2 ± 0.1	0.2 ± 0.05	0.19 ± 0.03	0.18 ± 0.02
Total D' (Gy/ka)	0.84 ± 0.12	0.68 ± 0.07	0.96 ± 0.13	0.78 ± 0.08	0.83 ± 0.08	0.92 ± 0.09
Age (years)	59 ± 15	1408 ± 196	124 ± 136	523 ± 138	2660 ± 270	4370 ± 470

Sample ID	CON09-8-4	CON09-8-25	CON09-8-48	CON09-8-81	CON09-8-105
D_e (Gy)	0.9 ± 0.1	2.05 ± 0.09	9.01 ± 0.33	14.53 ± 0.22	25 ± 0.4
n	29	19	38	40	30
Depth (m)	0.04 ± 0.01	0.25 ± 0.05	0.48 ± 0.05	0.81 ± 0.05	1.05 ± 0.05
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210
U (ppm)	1.18 ± 0.12	1.84 ± 0.18	1.24 ± 0.12	1.2 ± 0.12	1.38 ± 0.14
Th (ppm)	6.92 ± 0.69	9.24 ± 0.92	8.86 ± 0.89	10.45 ± 1.05	11.13 ± 1.11
K (%)	0.007 ± 0	0.001 ± 0	0.013 ± 0.001	0.008 ± 0	0 ± 0
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.2 ± 0.05	0.2 ± 0.04	0.19 ± 0.02	0.18 ± 0.02	0.18 ± 0.02
Total D' (Gy/ka)	0.82 ± 0.09	1.07 ± 0.11	0.93 ± 0.09	1 ± 0.1	1.06 ± 0.1
Age (years)	1096 ± 168	1921 ± 208	9650 ± 972	14490 ± 1407	23513 ± 2312

Sample ID	CON09-10-3	CON09-10-50	CON09-10-70	CON09-10-86	CON09-10-96	CON09-10-106
D_e (Gy)	0.13 ± 0.08	1.77 ± 0.05	3.57 ± 0.27	3.07 ± 0.14	2.86 ± 0.14	5.69 ± 0.13
n	82	77	82	75	36	59
Depth (m)	0.03 ± 0.01	0.5 ± 0.05	0.7 ± 0.05	0.86 ± 0.05	0.96 ± 0.05	1.06 ± 0.05
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210	150-210

U (ppm)	0.58 ± 0.06	0.97 ± 0.1	0.99 ± 0.1	1 ± 0.1	0.89 ± 0.09	1.04 ± 0.1
Th (ppm)	6.73 ± 0.67	13.72 ± 1.37	14.37 ± 1.44	13.12 ± 1.31	12.86 ± 1.29	15.31 ± 1.53
K (%)	0.025 ± 0.001	0.041 ± 0.002	0.041 ± 0.002	0.041 ± 0.002	0.033 ± 0.002	0.041 ± 0.002
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.2 ± 0.07	0.19 ± 0.02	0.18 ± 0.02	0.18 ± 0.02	0.18 ± 0.02	0.18 ± 0.01
Total D' (Gy/ka)	0.71 ± 0.09	1.18 ± 0.12	1.21 ± 0.12	1.14 ± 0.11	1.09 ± 0.11	1.26 ± 0.13
Age (years)	183 ± 115	1503 ± 158	2945 ± 373	2694 ± 296	2613 ± 292	4498 ± 474
Sample ID	CON09-13-2	CON09-13-20	CON09-13-40	CON09-13-55	CON09-13-65	CON09-14-17
D_e (Gy)	0.06 ± 0.02	0.2 ± 0.04	1.14 ± 0.44	2.27 ± 0.67	3.01 ± 2.25	0.25 ± 0.08
n	42	78	25	49	11	35
Depth (m)	0.02 ± 0.01	0.2 ± 0.05	0.4 ± 0.05	0.55 ± 0.05	0.65 ± 0.05	0.17 ± 0.05
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210	150-210
U (ppm)	0.89 ± 0.09	0.95 ± 0.09	1.01 ± 0.1	0.91 ± 0.09	1.02 ± 0.1	0.79 ± 0.08
Th (ppm)	10.45 ± 1.05	10.82 ± 1.08	15.96 ± 1.6	14.57 ± 1.46	16.44 ± 1.64	2.45 ± 0.25
K (%)	0.058 ± 0.003	0.066 ± 0.003	0.066 ± 0.003	0.058 ± 0.003	0.066 ± 0.003	0 ± 0
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.2 ± 0.1	0.2 ± 0.05	0.19 ± 0.03	0.19 ± 0.02	0.19 ± 0.02	0.2 ± 0.06
Total D' (Gy/ka)	1 ± 0.14	1.04 ± 0.11	1.33 ± 0.14	1.22 ± 0.12	1.35 ± 0.14	0.49 ± 0.07
Age (years)	57 ± 20	189 ± 40	856 ± 344	1854 ± 578	2226 ± 1681	513 ± 179
Sample ID	CON09-14-41	CON09-14-77	CON09-16-4	CON09-16-79	CON09-16-119	CON09-16-159
D_e (Gy)	0.55 ± 0.02	0.73 ± 0.04	0.24 ± 0.01	4.42 ± 0.14	14.59 ± 0.07	17.51 ± 0.17
n	74	43	75	75	75	37
Depth (m)	0.41 ± 0.05	0.77 ± 0.05	0.04 ± 0.01	0.79 ± 0.5	1.19 ± 0.5	1.59 ± 0.5
Min. grain size (mm)	150-210	150-210	150-210	150-210	150-210	150-210
U (ppm)	0.62 ± 0.06	0.7 ± 0.07	0.68 ± 0.07	0.64 ± 0.06	0.9 ± 0.09	0.84 ± 0.08
Th (ppm)	2.2 ± 0.22	2.76 ± 0.28	3.76 ± 0.38	5.19 ± 0.52	7.51 ± 0.75	9.98 ± 1
K (%)	0 ± 0	0.009 ± 0	0.025 ± 0.001	0.025 ± 0.001	0.025 ± 0.001	0.033 ± 0.002
Moisture (%)	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7	17 ± 7
Cosmic D' (Gy/ka)	0.19 ± 0.03	0.18 ± 0.02	0.2 ± 0.05	0.18 ± 0.12	0.17 ± 0.07	0.16 ± 0.05
Total D' (Gy/ka)	0.43 ± 0.04	0.48 ± 0.04	0.56 ± 0.07	0.62 ± 0.13	0.79 ± 0.1	0.91 ± 0.1
Age (years)	1271 ± 121	1527 ± 145	427 ± 51	7182 ± 1489	18580 ± 2398	19233 ± 2157

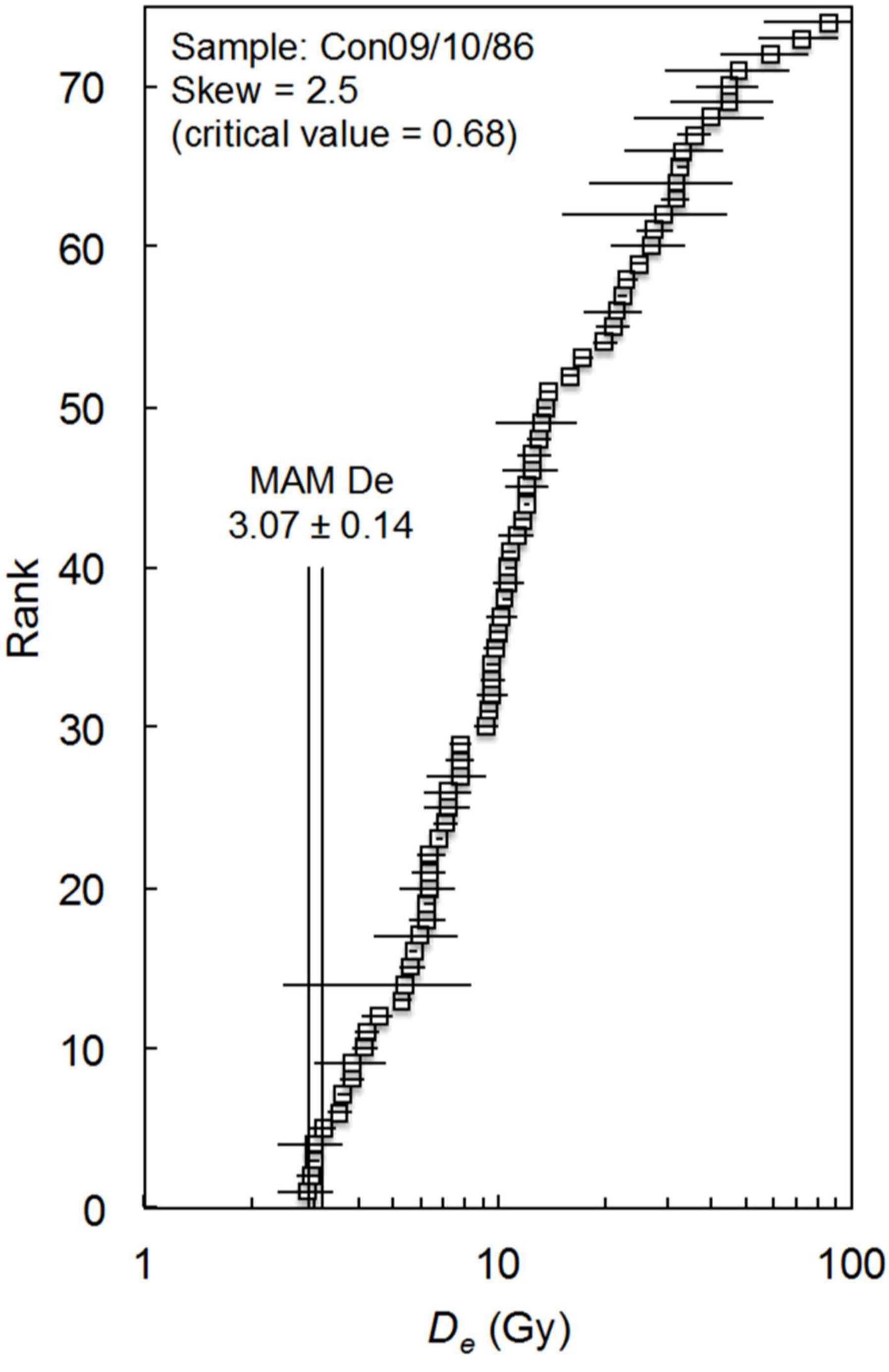
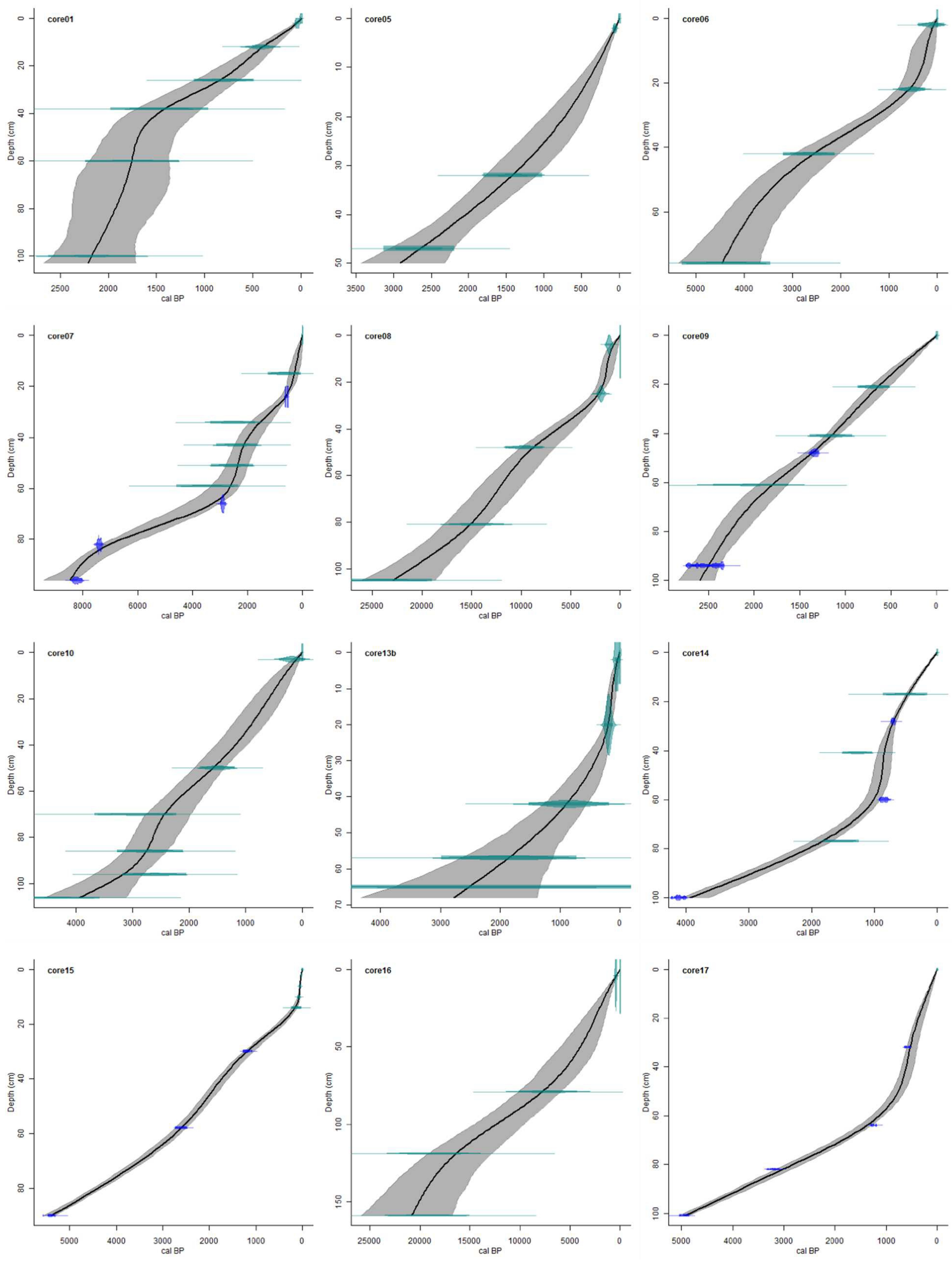
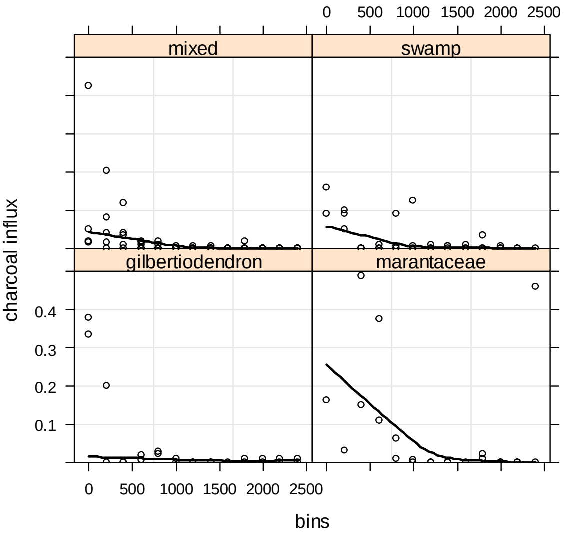


Figure A2. *Values of D_e (with 1 sigma errors) are shown ranked by D_e value, for sample Con09-10-86 (note the logarithmic D_e scale). The upper and lower bounds (1 sigma) of the Minimum Age Model (MAM) are indicated by the vertical lines. The 'critical value' given is the value beyond which the degree of observed skewness (for these data skewness=2.5, as shown) is statistically significant (at 95% confidence).*

Appendix 3. Age-depth models for each core run in CLAM. Light blue represent OSL dates except for Core15 where they are ^{210}Pb dates. Blue represents ^{14}C-AMS dates.



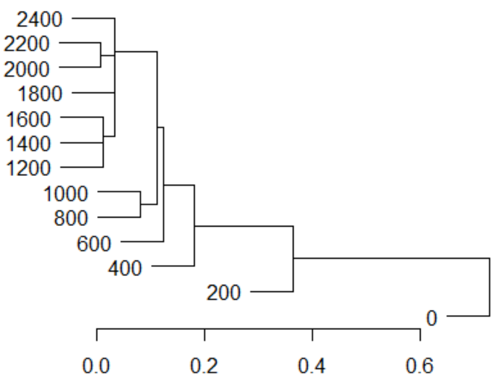
Appendix 4. Plots showing a non-linear temporal trend in charcoal influx per forest type. Bins in cal BP. Y axis was truncated at 0.5 rather than 3 (the maximum value) to observe trends.Appendix 5. Details of the additive models tested to relate charcoal influx to forest type and time



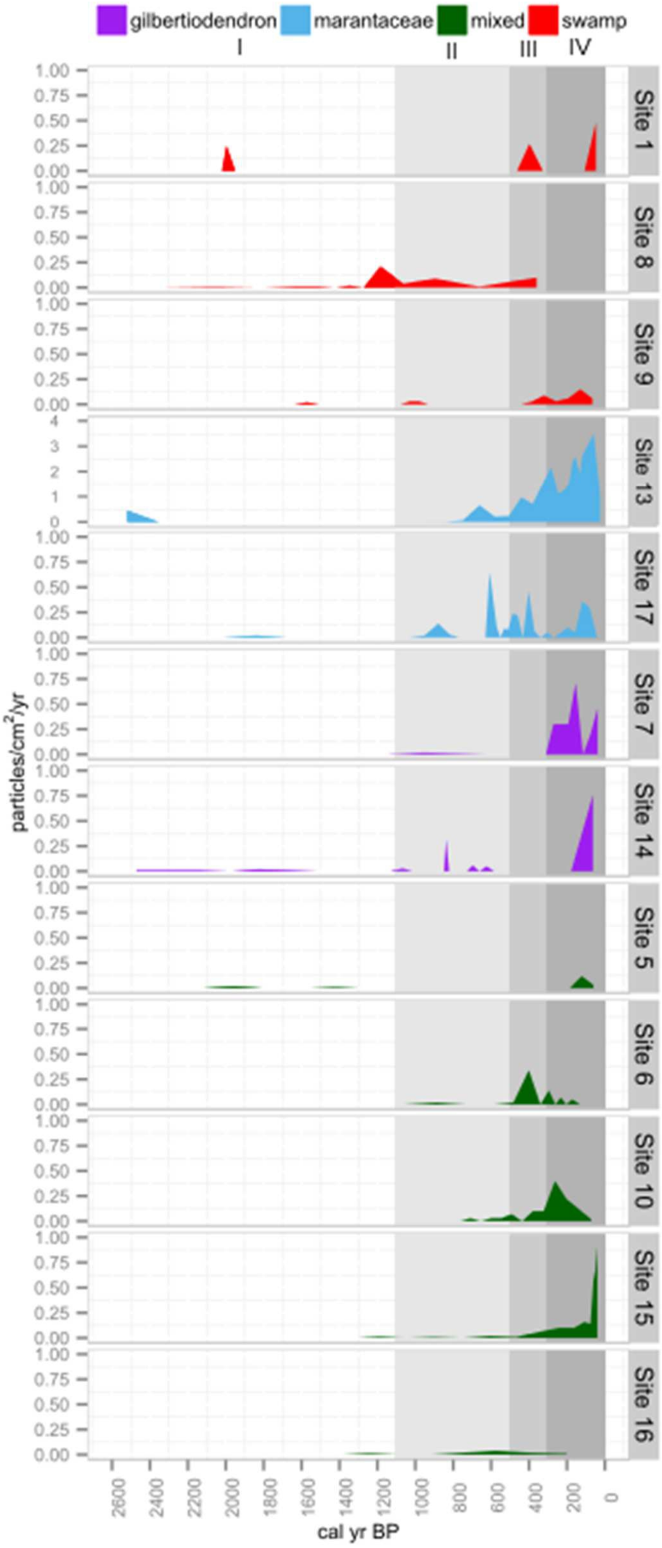
Appendix 5. Details of the additive models tested to relate charcoal influx to forest type and time (bin).

Model	Variance structure	Correlation structure	AIC	R-squared
Baseline	-	-	62.20	0.207
A	Different standard deviations per core. Formula: ~1 | core		-429.53	0.680
B	Different standard deviations per forest type. Formula: ~1 | forest_name		-316.57	0.408
C	Different standard deviations per forest type. Formula: ~1 | forest_name	Compound symmetry. Formula: ~bin	-314.75	0.410
D	Different standard deviations per forest type. Formula: ~1 | core	corAR1 Formula: ~bin	-427.53	0.680
E	Different standard deviations per forest type. Formula: ~1 | core	corAR1 Formula: ~ bin|core	-427.53	0.680

Appendix 6. Cluster analysis to identify periods (time-zones) where charcoal patterns are different. Method used: CONSLINK (constrained single-link analysis).



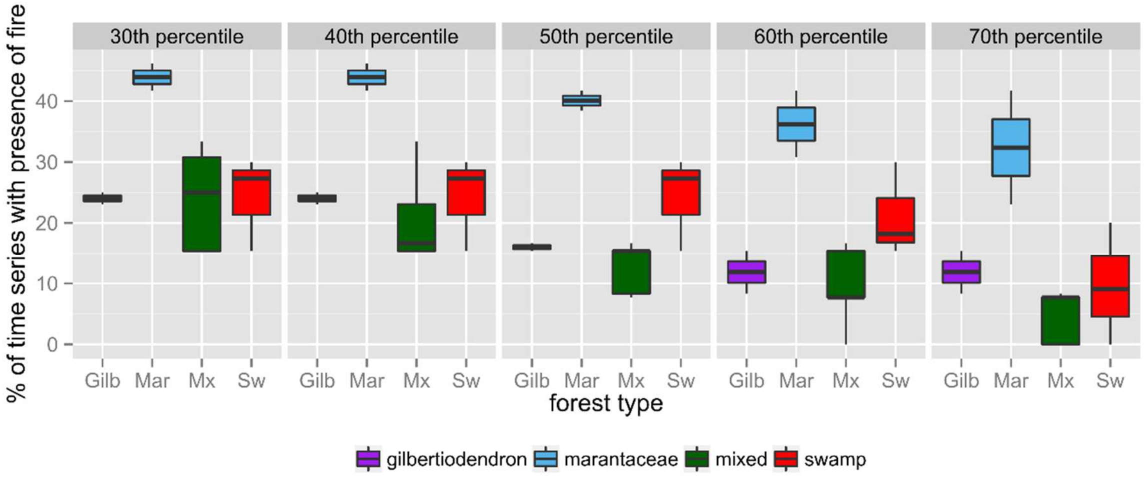
Appendix 7 Charcoal influx values for each core for the last 2500 cal BP (particles/cm^2/yr). The four different periods identified by using the zonation procedure with the 200-yr bin data (see Appendix 6) shown in Fig. 2 were overlayed: I) Minimal fires (2500-1100 cal BP), II) First occurrences of fires (1100-500 cal BP), III) Increasing fires (500-300 cal BP), IV) Highest peaks of charcoal (300-0 cal BP). Site 13 is shown at a different scale.



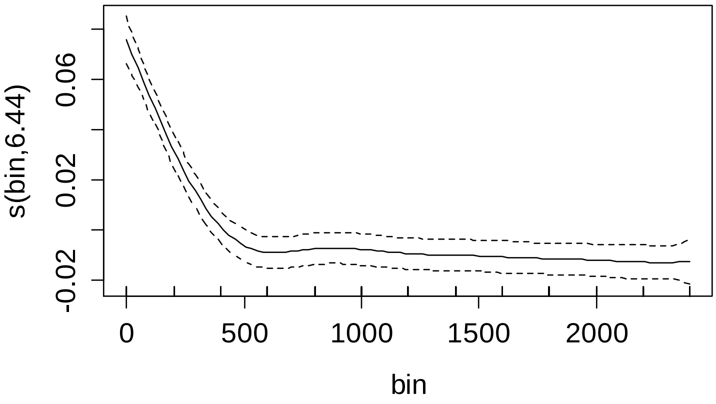
Appendix 8. *Spatial autocorrelation test (Moran's I) to assess if charcoal values were clustered, overdispersed or randomly distributed over space for each bin of 200 yr.*

Bin (range of cal BP)	Morans I	Z-scores (standard deviations)	p-value	Observations
0 – 200	-0.078	0.2339	>0.1	Random
200 – 400	-0.0403	0.5051	>0.1	Random
400 – 600	-0.1275	-0.0993	>0.1	Random
600 – 800	-0.0412	0.7147	>0.1	Random
800 – 1000	-0.3652	-1.4018	>0.1	Random
1000 – 1200	-0.144	-0.4986	>0.1	Random
1200 – 1400	-0.1881	-0.3950	>0.1	Random
1400 – 1600	-0.2165	-0.3753	>0.1	Random
1600 – 1800	-0.1924	-1.2124	>0.1	Random
1800 – 2000	-0.3364	-0.8974	>0.1	Random
2000 – 2200	-0.3556	-0.9976	>0.1	Random
2200 – 2400	-0.25	-1.1410	>0.1	Random
2400 – 2600	-0.0753	0.5472	>0.1	Random

Appendix 9. *Boxplots showing fire frequency per forest type based on number of 200-year bins with presence of charcoal. Different thresholds were used to define presence or absence of fire (30th, 40th, 50th, 60th, 70th percentiles of charcoal influx values) as a sensitivity analysis.*



Appendix 10. Estimated smoother for the GAMM (solid line) and the 95% point-wise confidence bands (dotted line). The horizontal axis represents the 200-year bin in cal BP and the vertical axis the contribution of the smother to the fitted values.



CHAPTER 3: MARANTACEAE AND DENSE FOREST: TWO ALTERNATIVE STABLE STATES IN CENTRAL AFRICA?

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Running headline: Alternative stable states in Central African forest

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SUMMARY

1. It has long been hypothesised that the Marantaceae forest from Central tropical Africa represents a successional stage between savannah and dense mixed-species forest. An alternative hypothesis is that some Marantaceae forest occurs where there has been a high frequency of forest fires. However, detailed analysis of the ecological mechanisms behind the forest-fire relationship and how it influences forest composition are still scarce.
2. We investigated the potential long-term coupling processes between forest and fire in the Marantaceae forest of northern part of the Republic of Congo. This forest type is characterized by an open canopy and abundant giant herbs from the family Marantaceae and Zingiberaceae. We put forward the hypothesis that the presence of Marantaceae forest is related to the frequency of fire rather than representing a succession from savannah to forest and that and that it represents an alternative stable state to dense forest.
3. To address this hypothesis, we extracted phytoliths (a vegetation proxy) and fossil charcoal (a fire proxy) from two sites containing sediment cores spanning 750 and 1250 cal BP collected in current Marantaceae forest.
4. Our results show a switch from a broad-leaved tree dominated community (dense forest) to a Marantaceae dominated community (Marantaceae forest) around 450- 600 cal BP; a change that has endured until present.
5. We found there was a significantly higher fire frequency in the period when Marantaceae forest dominated, compared to the earlier period when dense forest dominated. Our results point to a positive feedback between Marantaceae forest and fires and indicate that the mechanisms behind the maintenance of Marantaceae forest are more related to the opening of the canopy through fire than to the establishment of the Marantaceae forest via succession.
6. Synthesis: We tested the hypothesis of natural succession against human intervention through fires to explain the presence of Marantaceae forest, typical of Central Africa. Using a palaeoecological approach we showed the importance of fires in shaping this forest and in creating alternative stable states, providing important information for management practices.

Keywords: Congo basin, forest dynamics, Holocene, Marantaceae forest, palaeoecology and land-use history, paleofires, tropical forest.

INTRODUCTION

Marantaceae forest, typical of Western and Central African forest, is characterized by a sparse tree canopy and an understorey dominated by giant herbs principally from the family Marantaceae (arrowroot) and/or Zingiberaceae (ginger) (Aubréville 1948; Swaine 1992; White 2001b; Gillet 2013). These herbs can be found in old cleared land, open-forest undergrowth, road sides, etc (Letouzey 1986) and when they are present as a large thick understorey within sparse tree canopy, this vegetation structure is known as “Marantaceae forest”. The herbs of this forest are important food source for gorillas and elephants, especially during dry season, (Williamson *et al.* 1990; White *et al.* 1995) and are important nesting areas for gorillas and resting areas for buffalos (Devos *et al.* 2008; Melletti *et al.* 2009). An explanation for the presence of these large areas of Marantaceae forest is still under debate and several hypotheses have been proposed.

One hypothesis suggests that Marantaceae forest is a successional stage from savannah to dense forest, especially in areas where this forest type is surrounding enclosed savannahs such as in littoral Congo, Cameroon and Gabon (Letouzey 1968; de Foresta 1990; White 2001b). Here, the absence of fire after afforestation is suggested as the main driver of this recovery (White 2001b). However this hypothesis was discussed by Favier and colleagues who proposed instead that in the succession from savannah to forest, the presence of Marantaceae species may be due to opportunistic establishment after logging extraction (Favier, de Namur & Dubois 2004) rather than a simple savannah to forest succession. On the other hand, it is also known that Marantaceae forest is related to fires in Ghana and northern Congo (Swaine 1992; Brncic 2002) and areas currently covered by this forest type have shown higher frequency of fires in the past than areas currently covered by other forest types in the region of northern Congo (Tovar *et al.* 2014). Detailed analysis of the ecological mechanisms behind the long-term forest-fire relationship and how it influences the forest composition are still scarce for Central African forest.

In the tropics, fire acts as a trigger of vegetation change, either through one large event or several successive events (Cochrane 2003). During the Holocene, fires alone, presumably mostly caused by scattered human activities, have not caused forest disappearance in Central Africa or in the neotropics (Brncic *et al.* 2007, 2009; Bush *et al.* 2007; Urrego *et al.* 2013). However, evidence suggests that fires have caused changes in forest composition with the appearance of species after fire episodes that were not present before (Hart *et al.* 1996), an increase in pioneer species or non-pioneer light demanders (Brncic *et al.* 2007), or an increase in species associated with forest gaps and clearings (Bush *et al.* 2007).

Once the disturbance stops vegetation may recover its composition after a period of time that can span centuries in the case of tropical forest (Bush & Colinvaux 1994). Successive fires can also maintain certain vegetation compositions; post-disturbance vegetation may generate positive feedbacks with fire to perpetuate compositional changes leading to the existence of alternative stable states (Petraitis & Latham 1999). To study the persistence or disappearance of new forest compositions and the potential existence of fire-vegetation feedbacks, long-term records (centuries) that comprise more than one generation are required (Willis *et al.* 2010). Few long-term studies in tropical forests have addressed a detailed analysis of fire-vegetation interaction, and approaches have been more qualitative than quantitative. Most analyses rely on visual inspection of coincidences between peaks of charcoal and the different taxa rather than statistical analysis. Better projections of future fire impact on forest therefore require long-term studies that seek to understand the response of tropical forest to fires with more robust analyses.

This research aims to elucidate the potential existence of long-term coupling processes between forest and fire in Central Africa using the Marantaceae forest as a case study. We aimed to test the hypothesis that Marantaceae forest is not a succession from savannah to forest but a result of forest-fire interaction in the Sangha River region (northeast of Republic of Congo). In order to test this we studied the vegetation and fire history of the area where currently Marantaceae forest exists using a palaeoecological approach. We collected two sediment cores in two present day Marantaceae forest spanning between 750 and 1250 cal BP. Phytoliths were extracted from these sedimentary sequences to analyse the vegetation history, and fossil macroscopic charcoal to analyse fire history.

MATERIALS AND METHODS

Study area

The study area is located in the north east of the Republic of Congo (Fig. 1), an area covered by lowland moist forest. Total annual precipitation in the study area is around 1600 mm and the major dry season occurs between December and February (Harris 2002). Several “terra firma” forest types are present in this area, mixed species, broadleaf semi-evergreen dense forest (hereafter dense forest), monodominant *Gilbertiodendron dewevrei* forest, and Marantaceae forest (Harris 2002; Gillet 2013). This last forest type is defined here by the presence of species from the family Marantaceae (arrowroot) and Zingiberaceae (ginger) as a widespread, dense understory below a sparse tree canopy (Aubréville 1948; Letouzey 1968; White 2001b) where free-standing Marantaceae species may reach up to 5 m in height (Letouzey 1986). In our study area four subtypes of Marantaceae forest can be found based on the opening of the canopy and the herbs species (Gillet 2013):

a) Open vegetation with *Aframomum*: In addition to the Marantaceae species *Haumania liebrechtsiana* and *Megaphrynium macrostachyum,* the Zingiberaceae of the *Aframomum* genus is also present.

b) Sparse forest with *M. macrostachyum*: The majority of the understory herbs are *M. macrostachyum* and tree regeneration is rare.

c) Sparse forest with *H. liebrechtsiana*: The majority of the understory herbs are *H. liebrechtsiana* and tree regeneration is rare.

d) Dense forest with Marantaceae: Tree regeneration is present but the understorey is still occupied by dense patches of large layers of *H. liebrechtsiana* and *M. macrostachyum*.

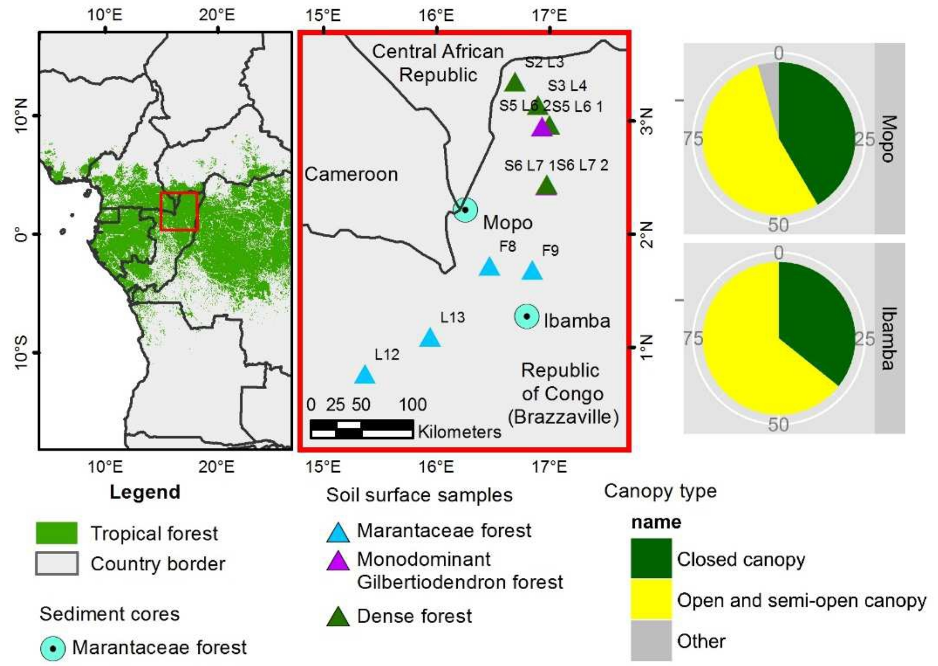

Figure 1 Study area. Location of soil surface samples from different forest types and core sites Mopo and Ibamba in present day Marantaceae forest. The graphs show the current percentage of closed canopy vs open and semi-open canopy based on satellite images (see Tovar et al. 2014) for each core location.

Collected material

We collected twelve soil surface samples in different forest types to assess the validity of using phytoliths as a proxy to identify Marantaceae forest: four in dense forest, two in monodominant *Gilbertiodendron dewevrei* forest, and six in Marantaceae forest. See full description of each forest type in Tovar *et al.* (2014). Samples were taken from different sites in northern Congo (Fig. 1), and two of the samples collected in the Marantaceae forest come from the core sites. The samples were taken in a 10 x 50 m plot by collecting 20 teaspoons of surface soil from across the plot which were then well mixed.

Two sediment cores were collected in areas currently covered by Marantaceae forest. The first core was collected in the site Mopo near Sangha river representing a mosaic of Marantaceae forest subtypes b and d (see previous section). The second one was collected in the Ibamba region, near Likouala-aux-Herbes swamps and the area is a mosaic of subtypes a and b (see Appendix S1 in Supporting Information for details of each site). Ibamba has a more open canopy than Mopo (Fig. 1). Age-depth models are shown in Table S2 in Supporting Information and the details of the dating are described in Tovar *et al.* (2014). We studied the first 40 cm (Mopo) and 63 cm (Ibamba) of each sediment core spanning 747 cal BP and 1243 cal BP respectively.

Phytoliths extraction and counting

Phytoliths are silica bodies present in cells of many plants that can be used to identify plant remains. They have been widely used to recognize species from the Marantaceae family, especially in the neotropics (Piperno 2006) although some African Marantaceae species have also been characterized (Runge 1999; Mercader *et al.* 2000). A phytolith reference collection was created by extracting phytoliths from leaves and stems of the most representative species of Marantaceae and Zingiberaceae in each site (see Appendix S1 in Supporting information). One cm^3 samples were taken at 2 cm intervals from the two sediment cores and from each soil surface sample. Samples were sieved using a 200 µm mesh. Sediment and soil samples were treated in the following way: 1) Carbonate removal using 15ml of hydrochloric acid, 2) Deflocculation using 15 ml of sodium pyrophosphate, 3) Organics removal using 20 ml of hydrogen peroxide while the tubes were in a hot bath, 4) Phytolith isolation using heavy liquid density separation (Sodium pyrithione) to allow phytolith flotation and recovery, 5) Adding microspheres to calculate concentration and influx (only for the sediment samples). Slides were prepared using oil immersion as a medium. Two hundred determinate phytoliths were counted for each sample to ensure a clear vegetation signal (Strömberg 2009).

Fire history

Macroscopic charcoal (> 150 µm) was used as a proxy of local fires (e.g. Clark 1988; Carcaillet *et al.* 2001). A sample of $1cm^3$ was extracted from the two sediment cores following the same sub-sampling used for the phytolith extraction. All particles were counted and charcoal influx (particles cm^{-2} yr^{-1}) was calculated by standardizing the number of particles by the sediment accumulation rate of each core. Detailed methods of this extraction are described in Tovar *et al.* (2014) where site 13 corresponds to Mopo and site 17 to Ibamba.

Statistical analysis

Current vegetation and phytolith composition: Recent evidence exist that some phytolith morphotypes are less stable thorugh time than others leading to different rates of degradation due to partial dissolution, but studies have mostly focus on crop species (Cabanes, Weiner & Shahack-Gross 2011; Cabanes & Shahack-Gross 2015). Incorporating such differential degradation in the analysis would require extensive laboratory testing of the decay rate of different phytolith morphotypes from rainforest species which is beyond the scope of this work. One way to overcome this issue is the use of broad vegetation groups that includes different morphotypes rather than a finer classification and thus, buffer the bias. Therefore, from the phytolith data of each soil surface sample we calculated the percentage of 7 main groups: Broad-leaved trees, Palms, Cyperaceae, Poaceae, Marantaceae 1, Marantaceae 2 and Marantaceae 3 (see Appendix S1 for a description of the three Marantaceae phytolith types). In order to group samples based on their similarity in composition we performed a hierarchical cluster analysis using the single linkage method. The dissimilarity matrix was calculated using the Bray-Curtis distance between the transformed values of the phytolith percentages (Hellinger transformation). Statistical analyses were performed in R v. 3.0.1 (R Development Core Team 2008) using the package vegan 2.0-10 (Oksanen *et al.* 2013).

Long-term changes in vegetation composition: We grouped the diagnostic phytoliths of the two sediment cores into five main groups: Broad-leaved trees, Cyperaceae, Marantaceae, Palms and Poaceae. Given the non-normal distribution of the phytolith percentage we used the Hellinger transformation which is known to deal with double-zeros in the data (Legendre & Birks 2012). A zonation procedure was applied by grouping together samples contiguous in time to define periods with characteristic compositions. For this we performed a cluster analysis using the constrained incremental sum-of-squares method (CONISS) that uses squared Euclidian distances as a measure of dissimilarity. In order to identify the meaningful number of zones we used the broken stick model (Bennett 1996). The cluster analysis and the broken stick model were performed in R v. 3.0.1 (R Development Core Team 2008) using the rioja package v.0.8-5 (Juggins 2013).

In order to identify the vegetation group that dominated each period we performed a principal component analysis over the transformed phytolith percentage (Hellinger transformation). An ordination biplot was used to observe changes from the meaningful periods identified in the zonation procedure. The ordination biplot was created by using the ggbiplot package.

Long-term changes in fire patterns: We assessed differences in fire intensity (charcoal influx) and fire frequency (percentage of fire occurrence) between the different periods identified in the vegetation analysis of sediments by using a Games-Howell test which deals with heterogeneity of variances and unequal sample sizes (Games & Howell 1976). Fire frequency was calculated as the percentage of samples for each period with presence of fires. In order to deal with uncertainty we defined 5 thresholds of charcoal influx value to decide presence/absence of fire (30th, 40th, 50th, 60th and 70th percentile of charcoal influx values for each core). We used the percentage of fires generated by each threshold for each period as samples to enter to the Games-Howell test.

Relation between components of Marantaceae forest and fire frequency: Marantaceae forest is characterized by an open canopy and the presence of Marantaceae species; therefore we analysed changes in phytoliths of broad-leaved trees (indicator of canopy) and Marantaceae species in relation to fire frequency using different time windows to explore the effect of previous fires on the vegetation. For each vegetation sample along the time series fire frequency was obtained as above using 5 percentiles as a threshold to decide the presence/absence of fire. We calculated the percentage of fire occurrence in the previous 50, 100, 150, 200 and 250 years to the age when the vegetation sample occurred. Due to the non-normal nature of the data we performed Spearman correlations exploring the relationship between fire frequency and the occurrence of Marantaceae abundance and broad-leaved abundance. We plotted each combination of frequency of fire and time window.

RESULTS

Identifying Marantaceae forest from phytolith composition

Phytolith composition of the soil surface samples shows three different types of Marantaceae phytoliths which do not have a one-to-one correspondence with present day species (see Appendix S1 in Supporting Information). Of the three types, Marantaceae 1 phytoliths are present only in samples collected in Marantaceae forest while phytoliths of Marantaceae 2 and Marantaceae 3 are also found in one sample of dense forest (see Figure S2 in Supporting Information). Marantaceae phytoliths were absent from *Gilbertiodendron dewevrei* forest. Total Marantaceae phytoliths ranged from 12% to 45% of phytolith composition in the samples from Marantaceae forest and around 6.5% in the sample collected in dense forest. Additionally the cluster analysis (Figure S2) aggregates all samples collected in Marantaceae forest in one group which confirms it is possible to identify Marantaceae forest from phytolith composition.

Changes in vegetation composition in two subtypes of Marantaceae forest over the last 1000 years

We identified 21 phytolith morphotypes in the two sediment cores (see Table S2 in Supporting Information) which were grouped into five main groups (see methods). Plots of percentages, concentration and influx of phytoliths of the main groups (see Figure S3 in Supporting Information) show these two last metrics seem to be affected by a degradation process. Lower values of concentration and influx are found in older periods than in younger periods precluding analysis of change in composition.Therefore, we performed the analysis of change in composition using percentages. Figure 2 shows the changes in vegetation.

The broken stick model determined two meaningful temporal zones (periods with distinctive vegetation) for each site. Mopo has a transition from period 1 (oldest) to period 2 (youngest) at 472 cal BP, while for Ibamba the transition occurs around 589 cal BP (Fig. 2). In both cases there is an increase in Palms, Cyperaceae and Marantaceae in the youngest period (period 2). Broad-leaved trees have decreased at both sites from an average around 81% during the oldest period to around 60% in average for the youngest period. Present day values show 36% of Broad-leaved phytoliths for Ibamba and 63% for Mopo. The extent of the decline is reflected in the current open-canopy forest at both sites, with Ibamba having a more open canopy than Mopo. Marantaceae first appeared around 450 cal BP at Mopo, reaching 3.5% of the current total species composition. At Ibamba it appeared 1000 cal BP, and Marantaceae species show two peaks at 8% dating around 450 and 100 cal. years BP (Fig. 2). Palms reached between 20 and 40% in the last 450-600 years at both sites.

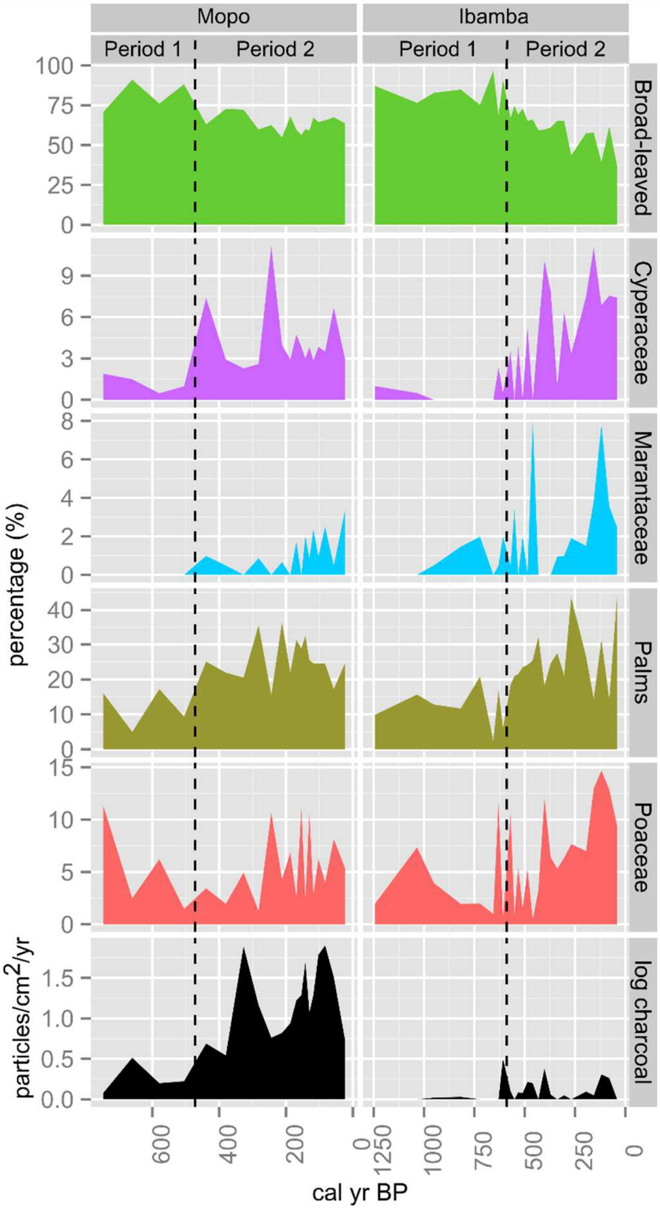

Figure 2 Change in percentage of phytolith composition. Charcoal influx is shown in the bottom in logarithm scale. Two periods are defined for each site, the threshold at site Mopo is 472 cal BP, and at site Ibamba it is 589 cal BP. Period 1 is the oldest period and period 2 is the youngest period for each site.

According to the PCA, samples that belong to period 1 at both sites (prior to 450-600 cal BP) are more related to broad-leaved tree dominated assemblages (Fig. 3). On the contrary, during period 2, after 450-600 cal BP, in both sites, species assemblages have a stronger presence of a combination of Marantaceae, Palms, Cyperaceae and Poaceae (Fig. 3). The first axis represents a gradient from low tree dominance to high tree dominance and explains 45% of the variance in species composition in Mopo and 57% for Ibamba. In total, the first and second axis explained more than 75% of the variance at both sites.

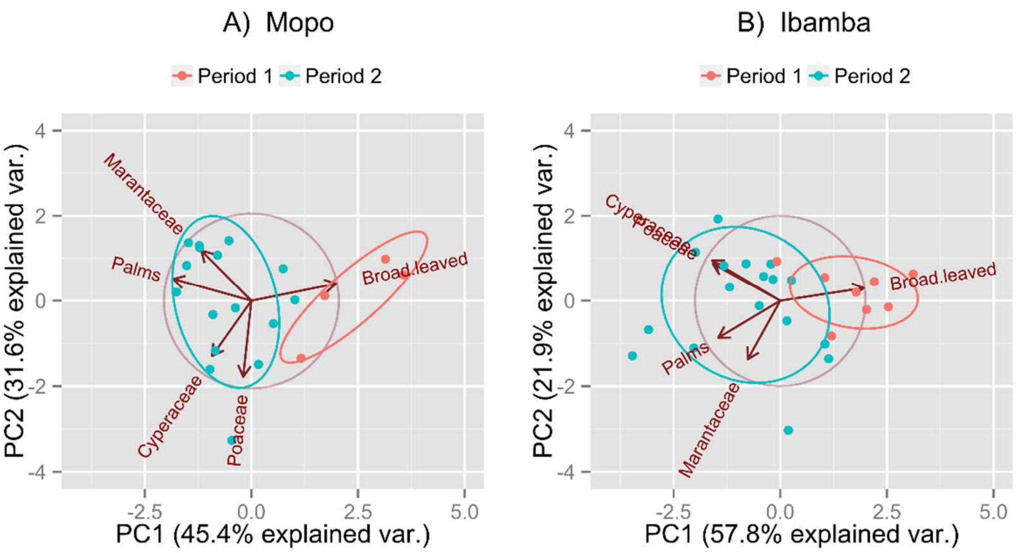

Figure 3 PCA for each site showing two periods with distinctive vegetation composition at each site. Samples belonging to the oldest period (1) are dominated by broad-leaved species, while those in the youngest period (2) are dominated by a combination of Marantaceae, Palms, Cyperaceae and Poaceae.

Comparing fire patterns between periods

Charcoal particles have been present for the whole time series of the sediment collected in Mopo, increasing considerably after around 450 cal BP (Fig. 2). At Ibamba, sediments show lower charcoal influx values than at Mopo and charcoal particles appeared at around 600 cal BP (Fig. 2). Charcoal influx values for Mopo range from 0.08 to 5.69 particles/cm^2/yr while for Ibamba they range from 0 to 0.65 particles/cm^2/yr.

In a comparison of charcoal influx (fire intensity) between the two identified periods for vegetation composition of each site we find that there is a significant difference between the two periods at Mopo (Games-Howell test, p-value = 0.013). No significant difference is found between charcoal influx values of the two periods identified for Ibamba (Games-Howell test, p-value = 0.62) (Fig. 4A). However, we find significant differences between the periods of each site for frequency of fires (Games-Howell test, Mopo p-value = 0.0001, Ibamba p-value = 0.002) (Fig. 4B) where values from the more recent period (period 2) show a higher fire frequency.

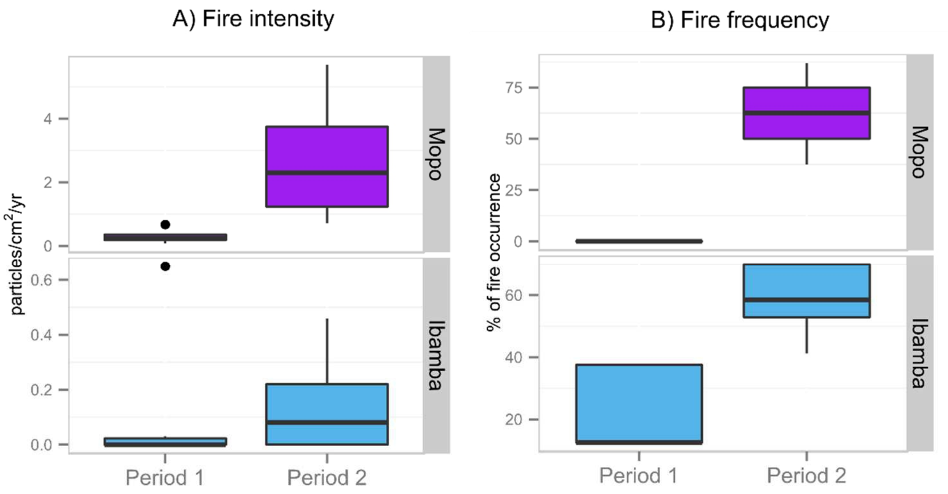

Figure 4 Differences in fire patterns between the two identified periods for each site. A) Differences in fire intensity were significant only for site Mopo (Games-Howell test p-value < 0.05) with a higher value in the youngest period (period 2) compared to the oldest. B) Fire frequency in the youngest period (period 2) was significantly higher than in the oldest period for both sites (Games-Howell test p-value < 0.05).

Main components of Marantaceae forest and frequency of fires

Our results show that the greater the opening of the canopy (lower percentage of broad-leaved tree phytoliths) the greater the frequency of fires at both sites (Fig. 5). At Mopo, which has a denser canopy than Ibamba, high frequency of fires in time windows of 50 to 150 years seems to have a higher impact than longer time periods (Fig. 5A). The significant correlation between fire frequency and openness of the canopy was found only when using the 30th percentile of charcoal influx values as the threshold to define presence/absence of fire in Mopo. In Ibamba, which has a very open canopy, the majority of time windows used for the analysis (100, 150, 200, 250 years) and all percentiles of charcoal influx values resulted in significant correlations with high fire frequency (Fig. 5B).

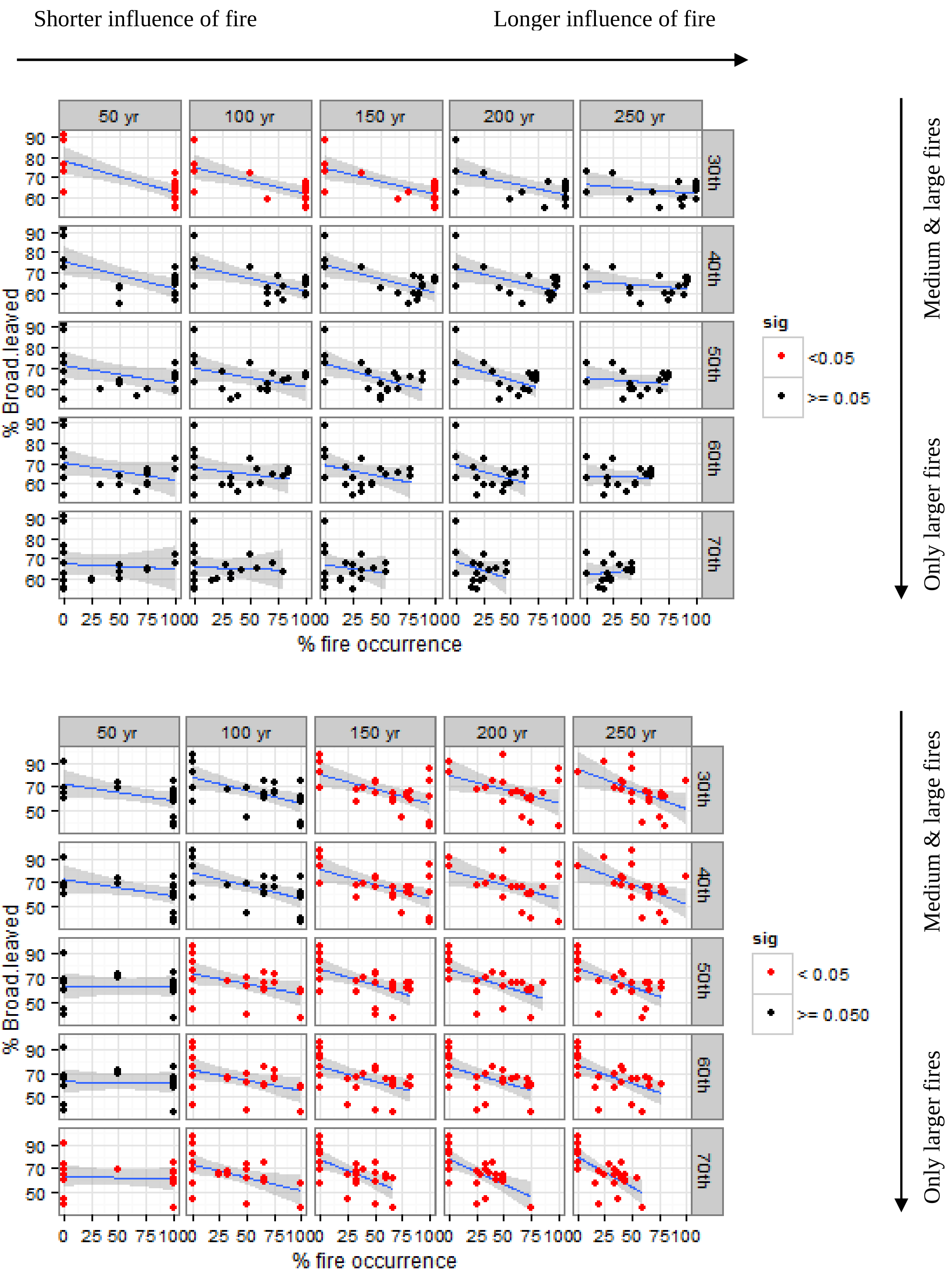

Figure 5 Percentage of Broad-leaved tree phytoliths against fire frequency for site Mopo (top) and site Ibamba (bottom). Columns represent fire frequency in the previous 50, 100, 150, 200 and 250 years (columns) of each phytolith value. Charcoal influx values were transformed to presence or absence of fire to calculate the percentage of fire occurrence based on different thresholds (30th, 40th, 50th, 60th and 70th percentile of the charcoal influx data in rows). From top to bottom the gradient indicates medium & large fires to only larger fires. From left to right a gradient from short influence to longer influence of fire is shown. Significant correlations in red, non-significant correlations in black (at a 95% of significant level).

In terms of the presence of Marantaceae species in relation to fire frequency we obtained contrasting results for the two sites (Fig. 6). At Mopo (Fig. 6A), where nowadays the main herb species is *M. macrostachyum*, higher frequency of fires in time windows between 100 and 200 years seems to be influencing higher abundance of Marantaceae species when charcoal influx values above the 30th, 40th, 50th or 60th percentiles were used to define presence/absence of fire. On the other hand, at Ibamba, where the current herbs layer includes the Marantaceae *M. macrostachyum*, *H. liebrechtsiana* and the Zingiberaceae *Aframomum sp*, there is no significant correlation between high fire frequency and high abundance of Marantaceae species (Fig. 6B).

DISCUSSION

Changes in vegetation and fire as part of a feedback system

Both sites show a change from a closed, broad-leaved taxa dominated forest to a more open canopy forest dominated by Marantaceae at around 450 to 600 cal BP. The change from dense to Marantaceae forest has persisted until the present. In this last 450-600 cal BP during the Marantaceae forest period, fire frequency has been significantly higher than during the dense forest period at both sites (Fig 4B). This suggests that higher fire frequency may be necessary to maintain Marantaceae forest.

But how could an increase in fire frequency act to maintain a different forest type? It is known that basal sprouting is one mechanism used by rainforest species to survive fire, and such sprouting is greater in burned areas than in other vegetation types or unburned forest (Marrinan, Edwards & Landsberg 2005; Knox & Clarke 2012). However, it has also been shown that a second fire one year later kills re-sprouting, meaning that fire frequency is a more important driver of lower tree regeneration than fire intensity (Ainsworth & Kauffman 2013). This seems to be the case in our study area. Fire kills re-sprouting and forest clearings are created after successive fire events where the Marantaceae herb *M. macrostachyum* has been shown to develop successfully (Brncic 2002).

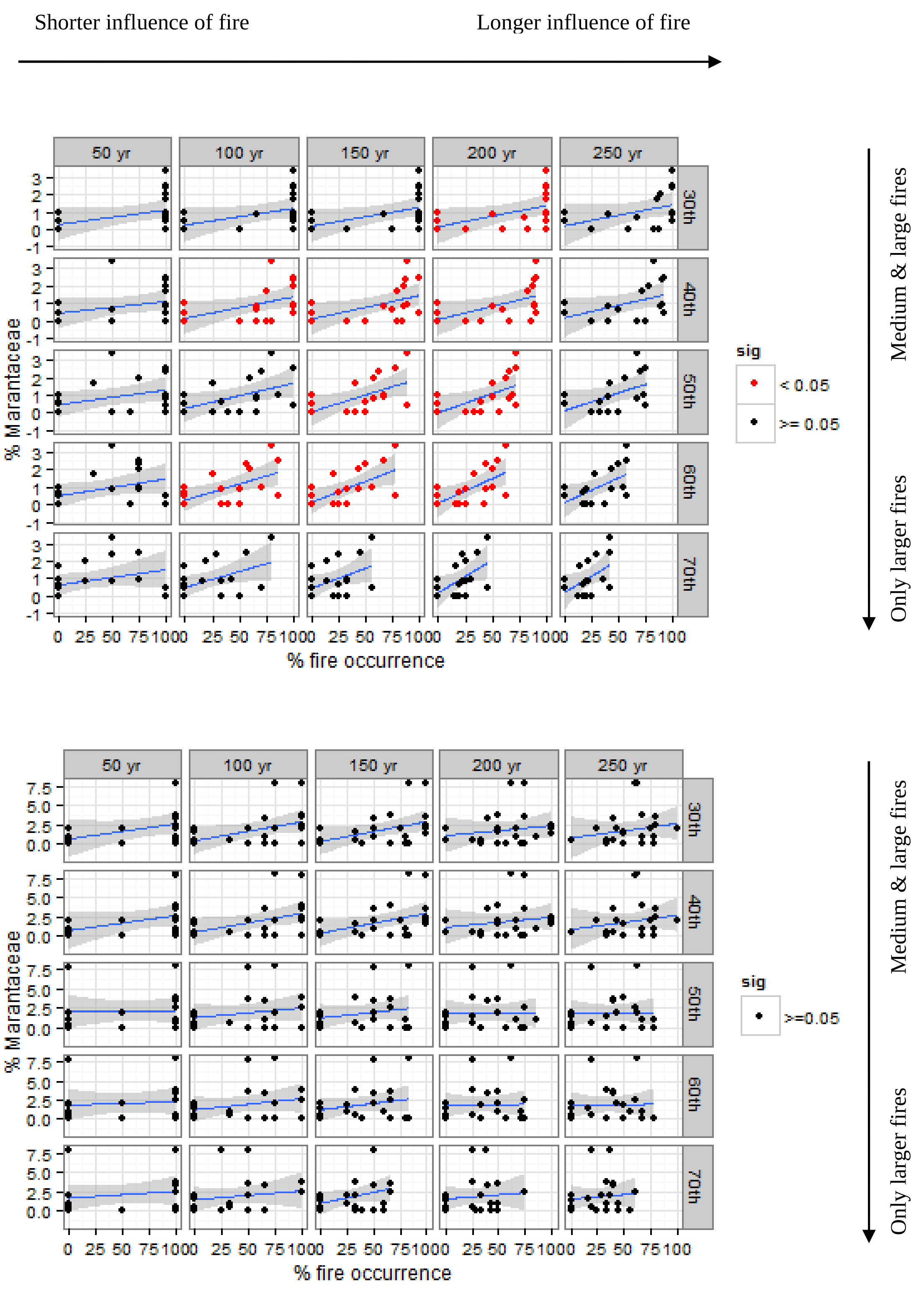

Figure 6 Percentage of Marantaceae species phytoliths against percentage of fire frequency for site Mopo (top) and site Ibamba (bottom). Columns represent fire frequency in the previous 50, 100, 150, 200 and 250 years (columns) of each phytolith value. Charcoal influx values were transformed to presence or absence of fire to calculate the percentage of fire occurrence based on different thresholds (30th, 40th, 50th, 60th and 70th percentile of the charcoal influx data). In red significant correlations and in black non-significant correlations (at a 95% of significant level)

In addition to the reduction in tree regeneration by fires, we suggest that species such as *M. macrostachyum* may also play a role in reducing the regeneration of broad-leaved tree species. A previous study has demonstrated that *M. macrostachyum* inhibits growth of tree seedlings from the soil seed bank due to shading (Brncic 2002). All this evidence points towards a fire-forest feedback where the post-disturbance vegetation may generate positive feedbacks with fire to perpetuate the new vegetation composition (Petraitis & Latham 1999).

A switch between states (change in plant species densities) that endures through time by positive feedbacks leads to the existence of alternative stable states (Petraitis & Latham 1999). Alternative stable states (two or more different vegetation types) are developed in the same environment and ideally in the same location (i.e. same climatic conditions and soil properties) (Petraitis & Latham 1999). The existence of alternative stable states as a consequence of fire has been described for rainforest/sclerophyll forest in North America and Australia (Hoffmann *et al.* 2009; Odion, Moritz & DellaSala 2010; Knox & Clarke 2012), and for rainforest/savannah in South America and Sub-Saharan Africa (Hoffmann *et al.* 2009; Staver, Archibald & Levin 2011). We propose that the Marantaceae forest that has existed in our study region for the last 600 years is not a result of a conversion from savannah to forest but an alternative stable state to dense forest.

We also propose that this alternative stable state seems to be maintained by high fire frequency and a positive feedback between fire and Marantaceae vegetation. Under this model, the two states (Mixed forest and Marantaceae forest) have their basins of attraction defined by their species composition. The basin of attraction of the mixed forest would be represented by close canopy, absence or minimal presence of Marantaceae species while Marantaceae forest's basin of attraction would be represented by open canopy, Marantaceae species. The basin of attraction of the Marantaceae state has a feedback interaction between Marantaceae taxa and fire. However, the external forces that cause the change from one state to the other couldn't be addressed with the current analysis.

Components of Marantaceae forest and fire

Canopy opening is one of the key processes in the formation of Marantaceae forest. We observed a reduction of broad-leaved tree phytoliths towards the present in the vegetation composition (Fig. 2). Our results show this decrease of arboreal species is correlated with high fire frequency (Fig. 5), something that has been shown for other tropical forest ecosystems over shorter periods (Eva & Lambin 2000). Our two sites represent two extremes of Marantaceae forest, one with a mix of dense and sparse canopy (Mopo) and the other with a mix of open and sparse canopy (Ibamba). Therefore, despite showing the same trend, we can observe a difference in the time windows affecting the canopy between sites where shorter periods of time (<150 years) affected the opening of the canopy in Mopo while longer periods (>100 years) affected Ibamba. In addition we also find a difference between the sites when considering high frequency of medium and large fires (30th percentile) or only considering the high frequency of large fires (70th percentiles). Disregarding the type of fire, Ibamba shows a significant correlation with high fire frequency while Mopo does not show correlation when only large fires were taken into account.

It is not clear what the underlying reasons are for the the difference between sites. One hypothesis is that a difference in human population size between sites creates a different interaction between fires and forest. A recent study show that soil pits collected near Mopo site contain much higher number of pottery shards than soil pits collected near Ibamba (Gillet 2013) suggesting a larger human population in Mopo than in Ibamba. Our results show the complexity of the relationship between the opening of the canopy and fire frequency. A higher temporal resolution analysis may help understanding the difference in sensitivity between sites.

The second key process in the formation of Marantaceaae forest is the presence of Marantaceae species. Our phytolith morphotypes represented mostly *M. macrostachyum* and *H. liebrechtsiana*. High fire frequency does not appear essential for the presence of these Marantaceae species, as only site Mopo shows a strong correlation between high fire frequency and the percentage of Marantaceae species (Fig. 6A). This suggests Marantaceae species in areas of dense canopy may require of fire to thrive while in a more open canopy area fire is not the main driver of Marantaceae species presence. Indeed, at Ibamba, Marantaceae species were present long before (1000 years ago) the change in vegetation occurred but the canopy was closed (average of 81% of broad-leaved tree phytoliths). Here, other mechanisms may have played a role in Marantaceae species establishment such as species competition or soil conditions. Soil studies performed in different Marantaceae forest around our site Ibamba near the Likouala-aux-Herbes swamps reveal soils are particularly poor and wet which may have facilitated the expansion of Marantaceae herbs and their maintenance during dry events (Gillet 2013).

The high presence of palms in the current vegetation at the two coring sites appears to be related to local conditions generated around the Sangha River. Soil surface samples collected from the core sites and those collected in Marantaceae forest along the Sangha River (Fig. 1) show the current presence of palms as part of the Marantaceae forest. However, two other surface samples (samples L12 and L13) collected in Lope, west to the Sangha River, did not contain palm photoliths. (Figure S2). At our two sites the presence of palms has been constant for all the analysed period. However, the percentage of palms may be overestimated as it is known that palms' production of phytoliths is large (Piperno 2006).

From the two main components of a Marantaceae forest we analysed, only the opening of the canopy is consistently related to the high frequency of fires in the two sites, while the presence of Marantaceae species may have also other drivers involve in addition to fire. The opening of the canopy is observed from the broad-leaved phytolith percentage and its clear decrease towards present time gives also support to reject the hypothesis of Marantaceae forest as a transition from savannah to forest.

Human dimension and management implications

It has been suggested that high fire frequency can promote greater resilience of forest coverage in tropical forest (Cole *et al.* 2014). Our results show that fire impacted the forest by opening the canopy and altering its composition, but that the forest itself did not disappear. Fires in our study area have been attributed to small slash and burn activities, rather than climatic-driven fire occurrence (Brncic *et al.* 2007; Tovar *et al.* 2014). Although these forests can survive frequent small-scale disturbance in terms of increased fire frequency (prehistoric human impact), they may not be resilient to modern forestry activities which have a greater impact on vegetation (Bush & Colinvaux 1994). Today, in addition to slash and burn agricultural activities, selective logging is present in our study area (Fayolle *et al.* 2014), which increases the pressure on the forest.

Forest clearance by slash and burning or logging activities create clearings that can potentially be colonized by the Marantaceae species such as *Megaphrynium macrostachyum* allowing the spread of Marantaceae forest (Brncic 2002). The observed change from dense forest to Marantaceae forest represents a loss of closed-canopy species. A recent study suggested that Marantaceae forest is a degraded type of *Celtis* forest covering a large area of northern Congo with a lack of trees with small diameter classes (Fayolle *et al.* 2014). The absence of young trees (regeneration) is attributed to the presence of giant lianas and herbs that prevent the development of trees seedlings (Brncic 2002; Fayolle *et al.* 2014). Tree regeneration in Marantaceae forest is almost non-existent and may only be re-established if the dense rhizome systems of the Marantaceae is broken and free space is available for tree seedlings (Gillet 2013). Based on our results, and under a scenario of future increases in fire frequency, it is possible that more dense forest will switch to Marantaceae forest. Management practices need to be aware of the feedback between Marantaceae forest and fire to prevent further degradation of dense forest (Fayolle *et al.* 2014).

In addition, the resilience of the forest to disturbance by fire may differ across the region. Site Mopo seems to be more sensitive to high fire frequency over shorter periods (50-150 years) than the southern site Ibamba, where effects are seen over a longer period (100-250 years). The importance of long periods between fires has also been observe in temperate rainforest. A study showed that in temperate rainforest where the time since the last fire is more than 75 years, the probability of having severely burned patches decreases, as does the size of burned patches in comparison to areas with shorter intervals since fire (Odion *et al.* 2010). In management terms, these figures may help as guidance to prevent frequent fires for these intervals of time. Future analysis with higher temporal resolution may help to elucidate a more specific number of fire events per interval of time.

CONCLUSIONS

Our results suggest that Marantaceae forest originated around 450-600 cal BP and has persisted to the present day in the region around the Sangha River. It is therefore an alternative stable state to dense forest instead of a successional stage in the change from savannah to forest as has been hypothesized before for Marantaceae forest in other regions. In this region, Marantaceae forest has endured for centuries and its maintenance appears to rely on the positive feedbacks between high fire frequency and the vegetation. The presence of Marantaceae forest as an alternative stable state is more closely related to the opening of the canopy than to the establishment of the Marantaceae species themselves, which seems to be affected by local factors in addition to fire.

These prehistoric human fires changed the dense forest to a mosaic with varying composition, but did not cause forest collapse. An increase in agricultural activities and the presence of logging activities may, however, put the current forest at risk of degradation. Notably, an increase in high fire frequency may cause more dense forest to switch to Marantaceae forest leading to the reduction of valuable forest tree species that are difficult to recover in a well-established Marantaceae forest. These species such as the African mahoganies (*Entandrophragma* spp.) are the basis for the economy of the region. Globally important populations of elephants, gorillas and chimpanzees will also be affected by a change to Marantaceae forest.

ACKNOWLEDGEMENTS

We would like to thank Ambroise Baker for his help during phytolith extraction. The cores were collected by Terry Brncic funded by the Leverhulme Trust. Soil surface samples were collected as part of the CoForChange project (www.coforchange.eu), funded by the ERA-Net BiodivERsA, with the national funders ANR (France). We are also thankful for permission and assistance from the Ministère de l’Enseignement Supérieur et de la Recherche Scientifique, Republic of Congo, Wildlife Conservation Society-Congo, PROGEPP, Congolaise Industrielle des Bois (CIB), Nouabalé-Ndoki National Park and Goualougo Triangle Ape Project.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods to create the phytolith reference collection.

Figure S1 Age-depth model of the sediment cores.

Figure S2 Phytolith composition of 12 soil surface samples representing 3 forest types (Dense, *Gilbertiodendron* and Marantaceae forest) and cluster analysis.

Figure S3 Temporal changes in species composition based on phytoliths for Marantaceae forest sites Mopo and Ibamba using percentages (A), concentration (B) and influx (C) phytolith values.

Table S1 Description of the two sites (Mopo and Ibamba) where sediment cores were collected.

Table S2 List of the phytolith morphotypes (diagnostic phytoliths) found in the two sediment cores.

Appendix S1 Methods to create the phytolith reference collection

Phytoliths were extracted from leaves and stems using the dry ashing method (500°C for 3 hours) (Parr, Lentfer & Boyd 2001) from the following species: *Megaphrynium macrostachyum* (leaf), *Sarcophrynium schweinfurthianum* (leaf), *Haumania liebrechtsiana* (stem), *Haumania danckelmaniana* (leaf), *Aframomum* sp (stem and leaf) to build a reference collection. For each reference sample we counted a minimum of 300 phytoliths ("Tot count" field in the table below) to identify the most prominent morphotypes for each species. Descriptions of types are provided in the same table. During analysis of the samples not all phytolith morphotypes were observed. The penultimate column of the table ("Final name in sample counting") is the final name assigned while counting and the one that is presented in the results. Pictures were taken using a Moticon camera (5 megapixels) at 100 x magnification. The scale bar in each picture represents 10 µm. Four phytolith types were found in the reference material, however, only three of them (Marant 1, Marant 2 and Marant 3) were present in the soil surface samples and the core samples. The four types are:

- Hat-shaped (Marant 1): Present in Marantaceae species *Megaphrynium macrostachyum*, *Sarcophrynium schweinfurthianum*, *Haumania liebrechtsiana* and *Haumania danckelmaniana*
- Druse-like (Marant 2): Present in Marantaceae species *Megaphrynium macrostachyum*, *Sarcophrynium schweinfurthianum* and *Haumania danckelmaniana*
- Rose-like (Marant 3): Present in Marantaceae species *Sarcophrynium scheinfurthianum*
- Small spheres (Marant 4): Present in Zingiberaceae *Aframomum* sp.

Phytolith images were collected from literature to identify the main phytolith morphotypes in the following groups: Broad-leaved trees, Palms, Cyperaceae and Poaceae (Alexandre *et al.* 1997; Runge 1999; Mercader *et al.* 2000; Bremond *et al.* 2005, 2008; Chandler-Ezell, Pearsall & Zeidler 2006; Piperno 2006; Gu *et al.* 2008; Neumann *et al.* 2009; Pearsall 2011).

Species	Plant part	Tot count	Sub name	Description	Size (um)	% sample	Final name in sample counting	Picture
Megaphrynium macrostachyum (Marantaceae)	Leaf	311	Phyto01	Hat-shaped	8-17	63	Marant1	A
			Phyto02	Druse like	13-20	37	Marant2	B
Sarcophrynium scheweinfurthianum (Marantaceae)	Leaf	306	Phyto01	Rose-like	25	42	Marant3	C
			Phyto02	Druse-like	24	12	Marant2	D
			Phyto03	Hat shaped	7-10	46	Marant1	E
Haumania liebrechtsiana (Marantaceae)	Steam	315	Phyto01	Hat shaped (bubbles in the bottom)	10-15	79	Not observed in samples	F
			Phyto02	Hat shaped		21	Marant1	
Haumania danckelmaniana (Marantaceae)	Leaf	319	Phyto01	Druse-like	10-15	60	Marant2	G
			Phyto02	Hat shaped	12-17	40	Marant1	H,I
Aframomum sp (Zingiberaceae)	Steam	328	Phyto01	Small spheres	3-8	100	Not observed in samples	J
	Leaf	331	Phyto01	Small spheres	3-8	100	Not observed in samples	K

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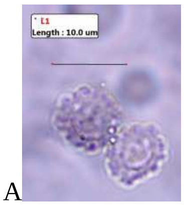

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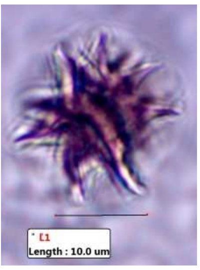

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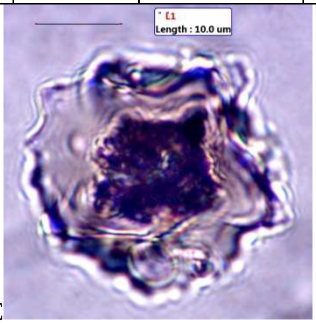

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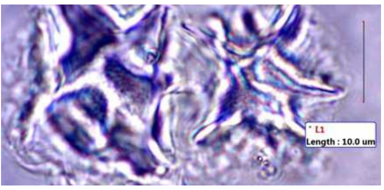

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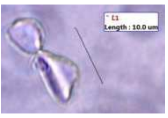

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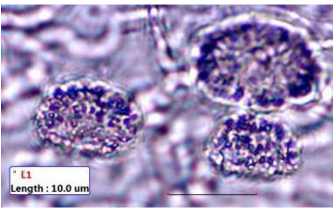

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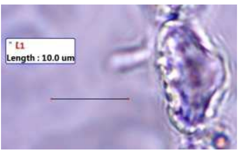

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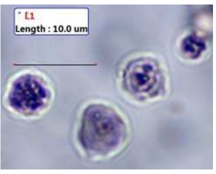

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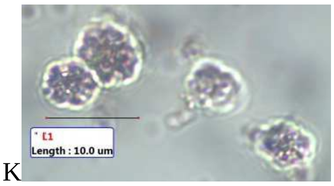

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Figure S1 Age-depth model of the sediment cores. Light blue represent optically stimulated luminescence (OSL) dates while blue represents ^{14}C-AMS dates. For detailed information of the dating procedure see Tovar *et al.* 2014.

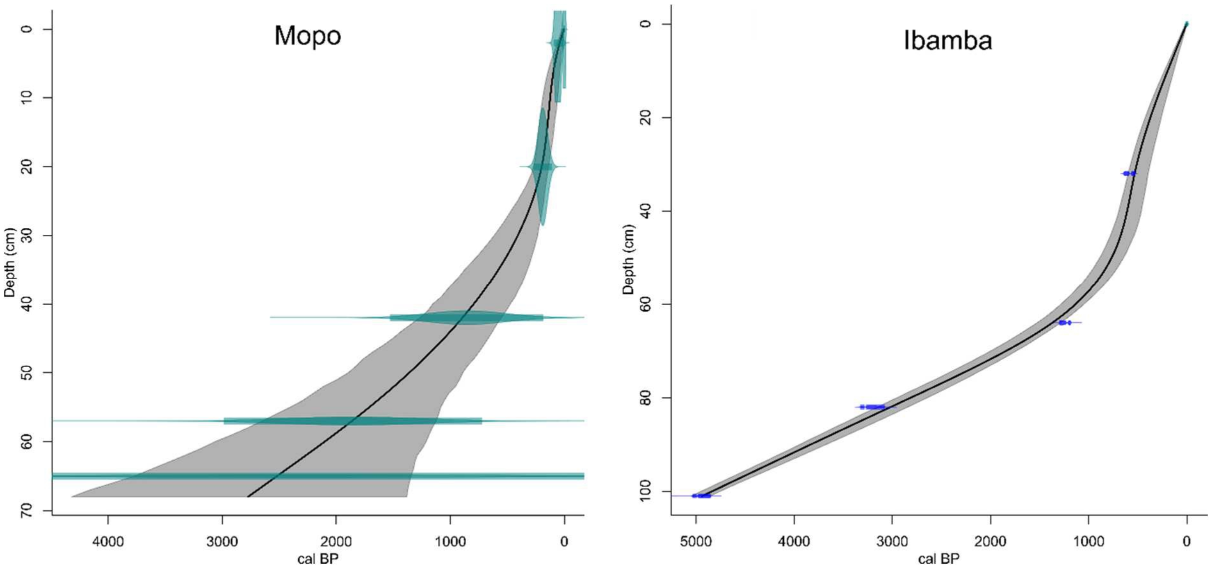

Figure S2 Phytolith composition of 12 soil surface samples representing 3 forest types (Dense, Gilbertiodendron and Marantaceae forest) and cluster analysis

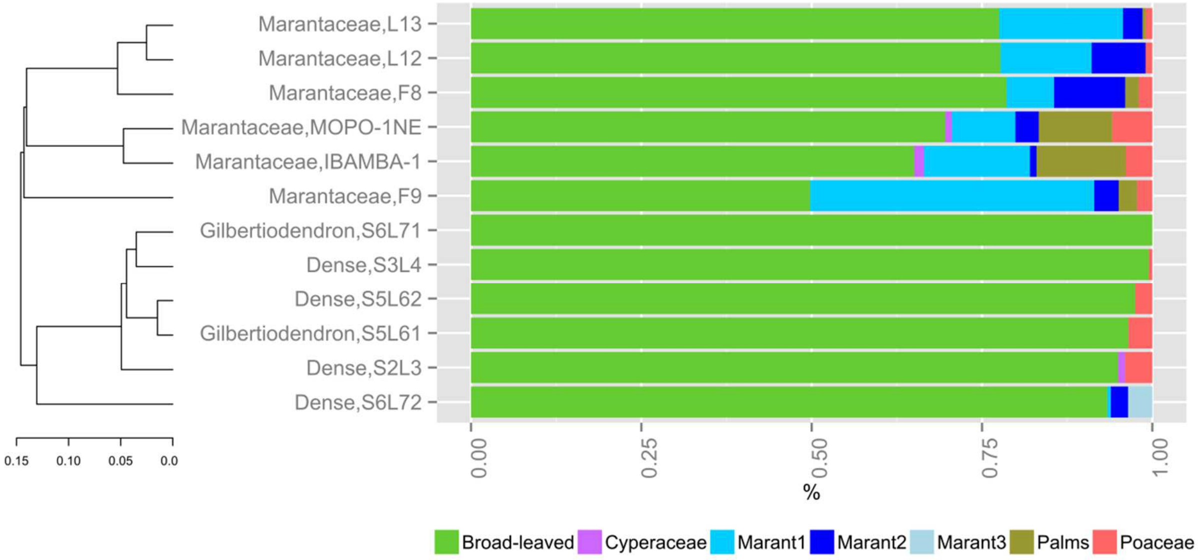

Figure S3 Temporal changes in species composition based on phytoliths for Marantaceae forest sites Mopo and Ibamba using percentages (A), concentration (B) and influx (C) phytolith values.

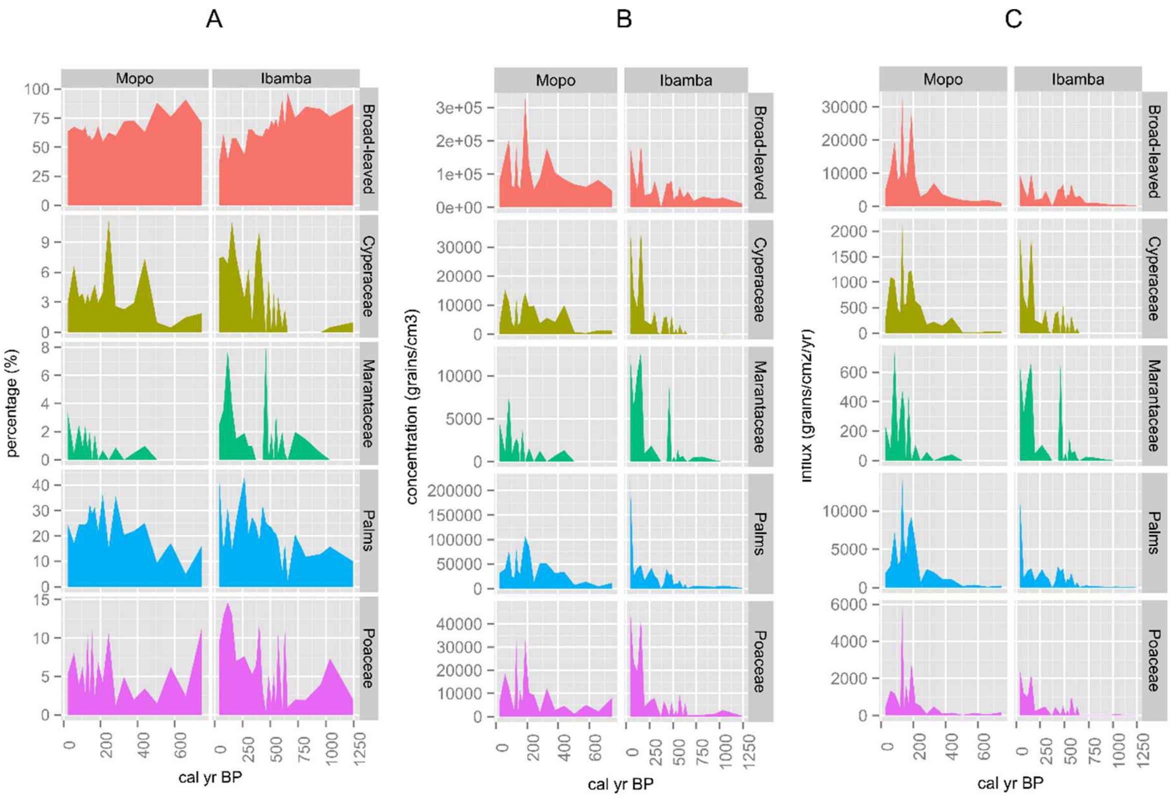

Table S1 Description of the two sites (Mopo and Ibamba) where sediment cores were collected

	Mopo	Ibamba
Longitude	16.2524 ° E	16.7970 ° E
Latitude	2.2141 ° N	1.2708 ° N
Elevation	378	338
Basin diameter	Yanga (35 x 50 m)	Yanga (150 x 150 m)
Main tree species	*Irvingia excelsa, Ricinodendron heudelotii, Entandrophragma cylindricum, Celtis mildbraedii, Terminalia superba, Guarea thompsoni, Staudtia kamerunensis, Eribroma oblongum, Zanha golungensis, Lecaniodiscus cupanioides, Pterygota bequaertii, Antrocaryon klaineanum*	*Terminalia superba, Dacryodes edulis, Ricinodendron heudelotii, Celtis mildbraedii, Tetrapleura tetraptera, Erythrophleum suaveolens, Diospyros mannii, Millettia laurentii, Chrysophyllum lacourtianum, Pycnanthus angolensis, Scottellia klaineana, Panda oleosa, Strombosia grandifolia, Strombosia pustulata, Garcinia punctata, Afrostyrax lepidophyllus, Pouteria altissima, Nauclea diderrichii, Entandrophragma cylindricum, Entandrophragma candollei, Guarea cedrata, Trichilia rubescens, Dialium angolense and/or polyanthum, Blighia*

		welwitschii, Myrianthus arboreus, Barteria fistulosa
Main tree pioneer species		*Aoranthe cladantha, Aoranthe nalaensis, Tetrorchidium didymostenon, Musanga cecropioides, Sterculia dawei, Macaranga spinosa, Croton haumanianus, Zanthoxylum gilleti, Macaranga monandra, Harungana madagascariensi*
Main Marantaceae and Zingiberaceae species	*Haumania danckelmaniana, Megaphrynium macrostachyum, Aframomum sp., Sarcophrynium schweinfurthianum*	*Haumania liebrechtisiana, Megaphrynium macrostachyum, Aframomum sp., Sarcophrynium schweinfurthianum*

Table S2 List of the phytolith morphotypes (diagnostic phytoliths) found in the two sediment cores

Phytolith name	Vegetation group	Mopo	Ibamba
Arecaceae	Palms	x	x
Acicular hair cell	Broad-leaved trees		x
Elongated with facets	Broad-leaved trees		x
Globular facetate	Broad-leaved trees		x
Globular granulate	Broad-leaved trees	x	x
Multifaceted blocky	Broad-leaved trees	x	x
Platelet polygon (> 5 edges)	Broad-leaved trees	x	x
Cyperaceae: Polyhedron	Cyperaceae	x	x
Hat-shaped	Marant1	x	x
Druse-like: Sphericals irreg folded surf	Marant2	x	x
Druse-like: Sphericals irreg folded surf	Marant3	x	x
Rose-like	Marant3		x
Bilobate	Poaceae	x	x
Cross	Poaceae	x	x
Cylindrical polylobate	Poaceae		x
Elongate echinate	Poaceae	x	x
Elongate smooth	Poaceae	x	x
Rondel	Poaceae	x	
Saddle	Poaceae	x	x
Trapeziform polylobate	Poaceae		x
Trapeziform sinuate	Poaceae		x

CHAPTER 4: *GILBERTIODENDRON* FOREST: MONODOMINANT FOREST RESPONSE TO DISTURBANCES

Article type: Original article

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ABSTRACT

Aim: The existence of monodominant forest in highly diverse tropical rainforest has been subject of large debate. Several mechanisms have been studied to explain its presence in African rainforest, but one hypothesis is that this monodominant forest persists under long-term minimal disturbance. Here we use a fossil record to test the past stability of current monodominant *Gilbertiodendron* forest and its relation to fire and climatic disturbances.

Location: Sangha River region, northern Republic of Congo.

Methods: We extracted fossil pollen from a sediment sequence collected in a landscape composed currently of monodominant *Gilbertiodendron* forest. The fossil record represents the vegetation history of the region over the past 2700 cal BP. Fossil charcoal was extracted to reconstruct fire history while climatic events for this period were reconstructed from other palaeoproxies published in the literature. We compared the vegetation history as detailed in this new sequence with two other published records collected in mixed forest and swamp forest to determine whether there was less disturbance evident over the past 2700 years in our site.

Results: Our results show that the monodominant forest has been present throughout the analysed period as recorded in our sediment. Fossil *Gilbertiodendron* pollen was found in every sample covering the interval from 2700 cal BP to present in similar percentages to present day soil surface samples. In addition no statistically significant change in species composition over this time was found using zonation techniques. This is despite the fact that significant climatic changes are known to have occurred in this region during this interval in time from other records in the literature. Throughout the entire period there is only little evidence of burning in the past 300 years in our sediment.

Main conclusions: Our results indicate a long-term stability of the monodominant *Gilbertiodendron* forest with no statistical significant changes in the species composition and only minimal recent occurrence of burning. The stability in species composition contrasts notably with climatic fluctuations (dry and wet periods) described for the region over the past 3000 years, which have led to changes in composition in other records collected within 30 km from our sediment record. Our results suggest that monodominant *Gilbertiodendron* forest is more resilient to climate fluctuations than previously thought and that this feature and lack of fire disturbance over the past 2700 years probably promotes its persistence.

Keywords: Central African rainforest, Congo basin, fossil pollen, past climate change, palaeofires, resilience.

INTRODUCTION

Tropical rainforests are characterized by their high species diversity but occurrence of mature rainforest stands or patches dominated by one or few species of trees exist in all tropical continents (Hart 1990; Richards 1996). Particularly in Africa, areas of monodominant forest (classical monodominance sensu Peh *et al.* 2011a) are larger than in any other tropical rainforest (Primack & Corlett 2005) and the dominant tree species belong in most of the cases to the sub family Caesalpinoideae of the family Leguminoseae (Peh *et al.* 2011a). In Central Africa, the presence of the monodominant forest of *Gilbertiodendron dewevrei* is common as patches among the mixed *terra firma* forest (hereafter mixed forest) (White 1983; Harris 2002). It occurs from Nigeria to eastern Democratic Republic of Congo (DRC) but it is most common and forms the largest stands in an arc from south-eastern Cameroon to north-eastern DRC (Harris 2002). This is a shade tolerant species with large and apparently poorly dispersed seeds (Hart *et al.* 1989).

Over the past decades a number of hypotheses have been proposed to explain the existence of large patches of monodominant *Gilbertiodendron* forest in the African rainforest, These have included abiotic conditions (e.g. special soil characteristics), interactions with other species (e.g. resistance to pathogens, less seeds predation of *Gilbertiodendron*, association with fungi) and species traits (e.g. shade-tolerant juvenile *Gilbertiodendron,* more leaf litter production, slower rate of decomposition). Many of these hypotheses have subsequently been rejected. For example, there is no evidence of differences between soil characteristics from the *Gilbertiodendron* forest and the adjacent mixed forest (Peh *et al.* 2011b). Differences in pathogen damage (Gross *et al.* 2000) or seeds and juvenile predation (Hart *et al.* 1989) between monodominant and mixed forest were not found either. Lastly, the presence of ectomycorrhizal association does not seem to be the overall cause of monodominance, as other species such as members of the genus *Manilkara* also have this association and do not form monodominant stands (Torti, Coley & Kursar 2001).

Recently a framework has been proposed to integrate all possible mechanisms discussed in the literature that lead to monodominance. These includes the different species traits mentioned above and the presence of ectomycorrhizal interacting in a complex web for several tree generations and under low levels of disturbances (Peh *et al.* 2011a). Support for the mechanism of long-term minimal disturbances comes from the observation of a lower number and smaller sized gaps in the monodominant forest compared to the mixed forest (Hart *et al.* 1989). Together with the shade-tolerant juveniles of *Gilbertiodendron* that competes better under low levels of light and thus closed-canopy, this suggests that low disturbances may be necessary to maintain monodominant forest. However, to our knowledge, this long-term persistence under minimal disturbance has only been inferred but not yet tested.

Climatic and fire disturbances have been most frequently described in different long-term studies from the Central African rainforest. A major climatic disturbance has been documented at around 3,000-2500 cal BP, consisting of a decrease in precipitation (Ngomanda *et al.* 2009b; Schefuß *et al.* 2011) and leading to a major decrease of evergreen forest species in most sites (see Bonnefille 2011 for a review). After this regional climatic event, different periods of increased or reduced precipitation have been described for the last 2 millennia, although events were not always synchronous between sites (Nguetsop *et al.* 2004; Ngomanda *et al.* 2005; Brncic *et al.* 2007, 2009; Hubau *et al.* 2013).

Fires have been less explored for the Congo basin than climate, but different studies confirm that they occurred in the rainforest, either related to human activities in the last 1000 cal BP (Brncic *et al.* 2007, 2009; Tovar *et al.* 2014) or related to a drier climate (Hubau *et al.* 2013). In general, these studies suggest that fires were scattered and no major regional fire events have been described (Hart *et al.* 1996; Hubau *et al.* 2013; Tovar *et al.* 2014). Since results to date suggest neither a stable climate nor disturbance regime in the Congo forest – both thought to be prerequisites for development of monodominant forest blocks - the question arises of when monodominant rainforest formed and how they responded to disturbances.

In this study we used the currently monodominant *Gilbertiodendron dewevrei* forest of northern Congo as a case study to address two specific questions: 1) For how long has the monodominant forest been present in this area? 2) Over time what has been the relationship between the monodominant forest and climatic and fire disturbances? We addressed these questions using a palaeoecological approach where we; i) collected soil surface samples to explore present pollen representation in monodominant forest and adjacent mixed forest areas, ii) analysed the fossil pollen composition of a sedimentary sequence collected in a nowadays monodominant *Gilbertiodendron* forest spanning 2,722 cal BP, iii) analysed macroscopic fossil charcoal to explore fire patterns and, iv) compared our record with two other pollen records collected within the same region in mixed forest and swamp forest to analyse spatial responses to fire and climate, and v) compared the climatic disturbances described from other palaeo-proxies from the literature to our results.

MATERIALS AND METHODS

Study area

Our study area is located in the Sangha River region, in the north of the Republic of Congo (Figure 1). In this region *Gilbertiodendron dewevrei* forest (hereafter monodominant forest) is characterized by the high presence of the gregarious tree *Gilbertiodendron dewevrei*, a high shade tolerant species. Large seeds of about 5.5cm of length, and a weight of around 26-30 g makes its ballistic dispersal very poor with maximum dispersal distances between 5-10 m from the crown (Hart 1985; Blake & Fay 1997). The monodominant forest mostly occurs alongside streams and rivers forming patches (Harris 2002) and the continuous closed canopy of *G. dewevrei* reaches

30-45 m of height showing a lower number of species per fixed unit area than in the adjacent mixed forest (Harris 2002; Peh *et al.* 2014). Common large trees found in the monodominant forest are *Albizia gummifera*, *Anonidium mannii*, *Chrysophyllum pruniforme*, *Diospyros mannii*, *Irvingia excelsa*, *Irvingia robur*, *Manilkara mabokeensis* and *Tessmannia africana*. Total annual precipitation ranges from 1500-1600 mm (Harris 2002).

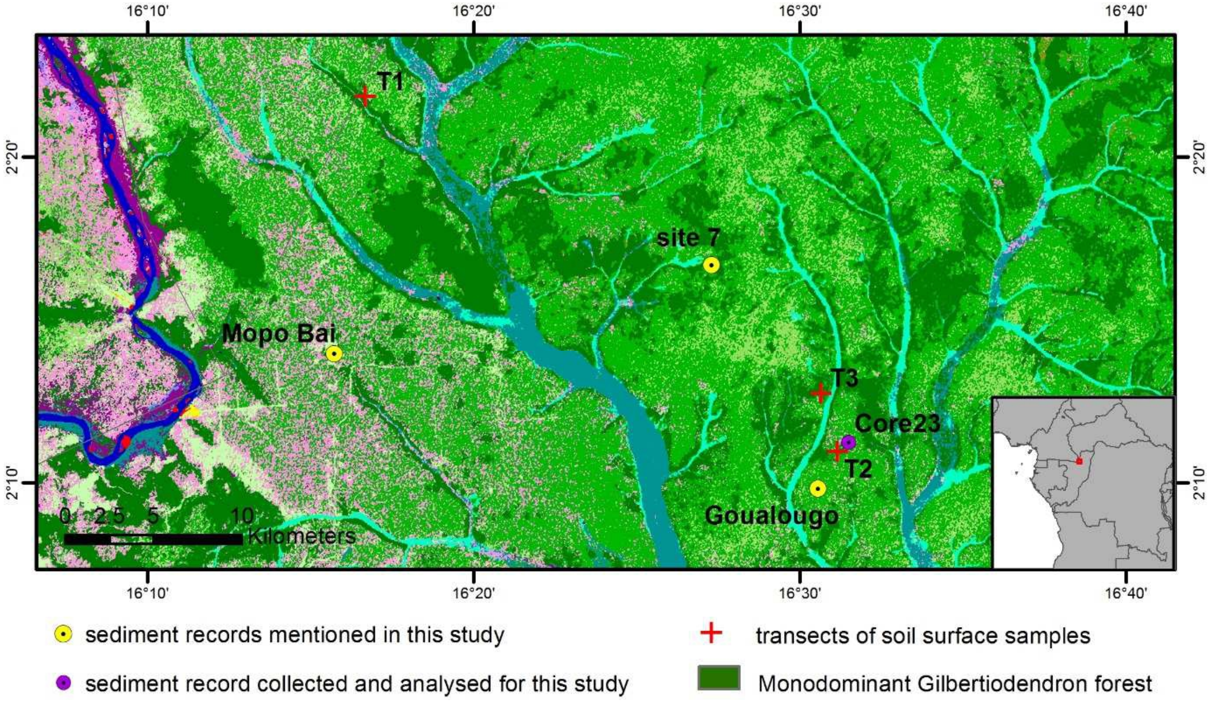

Figure 1 Study area. Location of the sediment core collected for this study (Core23), the location of the transects where soils surface samples were collected and the location of other two published pollen records that are used for comparison for changes in vegetation composition (the mixed forest Goualougo record and the swamp forest Mopo Bai record).

Collected material

Twelve soil surface samples were collected in the monodominant forest patches and their surroundings to analyse modern pollen rain in relation to vegetation composition. The sampling design included 4 repetitions of the following arrangement in a transect from inside the monodominant patch across the boundary and into the mixed forest: one sample inside the monodominant patch, one in the edge between the monodominant forest and the adjacent mixed forest, one in mixed forest at around 50 m from the edge of the *Gilbertiodendron* patch and one more at around 100 m from the edge. In total we sampled 3 transects (Figure 1). Transect 2 corresponds to the patch where the sediment core was collected (see next paragraph). Each soil sample consisted of approximately 200 g, collected in a 10 x 10 m square plot after removing litter.

A sedimentary sequence, Core23, was collected from a small lake (100 m diameter) at 2.18726°N, 16.52513°E close to the Goualougo research camp, using a Livingston corer with a tube diameter of 6 cm. Around the small lake, the first 10 m of land are characterized by shrubs. After those 10 m a dense *Gilbertiodendron* patch expands for more than 100 m. We extracted pollen from the first 32cm of the core spanning the last 2722 cal BP. For the sediment chronology we extracted three samples at different depths (14cm, 34cm and 52cm) that were analysed by the CHRONO Centre of Queen’s University Belfast to obtain AMS ^{14}C dates. Results for each depth were respectively 802±33 BP, 2834±42 BP, and 4699±40 BP. We used the CLAM software (Blaauw 2010) to established a continuous chronology of the core fitting a linear interpolation model. The age depth model is shown in Figure S1.

Pollen extraction and counting

Fossil pollen were extracted from soil surface samples and from the sediment. The sediment was subsampled every two centimetres. We followed the standard procedure for pollen extraction (Bennett & Willis 2001). For each sample of the sediment record at least 300 grains were counted excluding Cyperaceae and Pteridophyta spores (monolets and trilets). Pteridophyta and Cyperaceae were not included in the pollen sum. Pollen taxa were identified by using the African pollen reference collection from the Long Term Ecology Laboratory of University of Oxford and the reference collection held at the Palaeoenvironmental Change Research Group, Open University. Various references were also used for pollen identification (Maley 1970; Sowunmi 1973, 1995; Ybert 1979; Salard-Cheboldaeff 1981; Gosling, Miller & Livingstone 2013).

Charcoal analysis

Macroscopic charcoal (>150µm) was extracted from the sedimentary sequence as an indicator of local fires (Clark 1988; Whitlock & Millspaugh 1996; Carcaillet *et al.* 2001; Duffin *et al.* 2008). The same subsampling was applied as for pollen extraction. All charcoal particles within the sample were counted. We then calculated charcoal influx values (particles/cm^2/yr) by dividing the number of particles by the sample size (cm^3) and by the accumulation rate (yr/cm) calculated by the CLAM software.

Statistical analysis

Compositional and ordination analysis for soil surface samples

We calculated the percentages of pollen grains per taxon and plotted the most important species (>5% of pollen sum) for each transect against the sample type (within monodominant patch, edge, 50m and 100 m). We also performed a principal component analysis (PCA) of the pollen composition to explore affinities of species with certain samples. The following settings were used in the CANOCO software (ter Braak & Smilauer 2002): inter-species correlation, species score divided by standard deviation, square-root transformation and scores centred by species.

Temporal analysis for the sediment record

We plotted the most important species (those with at least one sample showing values equal or higher than 1.5% of pollen sum) against time in our pollen diagram. We grouped them according to the light and water requirements in the following categories: hydrophilic, light demander and shade bearers using references and personal expertise for this (Hawthorne 1995; Harris 2002; Brncic *et al.* 2009). Species for which this information was not available were classified under the category of others. In order to obtain significant thresholds in time to define periods when vegetation composition had particular patterns, two zonation techniques were applied. This process consists of clustering adjacent samples into successively larger groups using a dissimilarity matrix between pairs of samples. We first used the optimal partitioning approach by selecting the optimal splitting by information content implemented in PSIMPOLL 4.27 (Bennett 2007). Then, we applied an agglomerative technique by using the function chclust (constrained hierarchical clustering), method CONSLINK from the Rioja package in R. In both cases the broken stick model was used to assess the number of meaningful zones (Bennett 1996).

Analysis of vegetation composition and fires

In order to relate fires with species composition we performed a Canonical correspondence analysis (CCA) in the CANOCO software (ter Braak & Smilauer 2002) using charcoal influx values as environmental variable. Species percentages were square root transformed and we used inter-species distances. A Monte Carlo permutation was used to test the significance of the charcoal in explaining composition using a confidence level of 95%.

Comparison of Core23 with other sediments collected within the region

We compared the vegetation history of Core 23 with two other published sediment records collected in Goualougo (Brncic *et al.* 2007) and in Mopo Bai (Brncic *et al.* 2009), located within 30 km from Core23 and covering approximately the same interval in time (Figure 1). The Goualougo core was collected in a mixed forest site, and the Mopo Bai core was collected in a swampy depression, within mixed forest. Original diagrams are shown as supplementary information (Figure S2 and S3). In both sediments, changes in the composition of vegetation were found and attributed to climatic and fire disturbances. We performed the same zonation analyses as applied to Core23 to the data of these two cores, in order to compare the changes in composition between the three forest types (monodominant, mixed and swamp forest). Additionally, we performed an exploratory analysis of composition of the three cores together using a PCA to observe the trajectory of changes through time for the three records using the CANOCO software (ter Braak & Smilauer 2002).

Finally we described the main dry climatic events registered in the records from Mopo Bai and Goualougo based on geochemical analysis and in other palaeorecords studied in the Central African rainforest to analyse the responses of Core23 to these climatic disturbances.

RESULTS

Pollen spectra from current vegetation in monodominant forest patches and surroundings

Results show that pollen of *Gilbertiodendron* type *dewevrei* represent between 3.8% and 6% of the pollen count in soil surface samples collected within the monodominant forest patch (Figure 2). No pollen grains of this species were found in samples collected beyond the patch (50 and 100 m from edge). Axis 1 and Axis 2 of the PCA biplot account for 39.1% of the variability and show that pollen composition of samples collected within monodominant forest patches share similar species (Figure S4). These samples have a higher affinity with *Gilbertiodendron*.

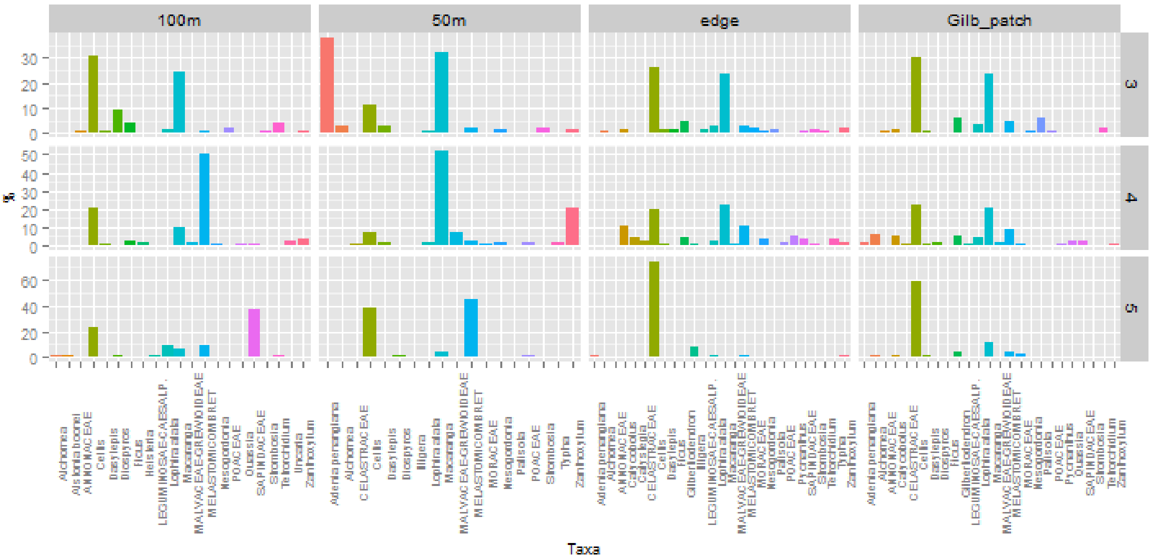

Figure 2 Pollen spectra of soil surface samples. Four samples in each of the three transects: one within the current monodominant forest patch (Gilb_patch) and three in the adjacent mixed forest (edge of the patch, 50 m of the patch edge and 100 m from patch edge).

Vegetation and fire history of what is at present a monodominant patch

Species showing the highest percentages along the sediment sequence are the light demanding taxa *Alchornea, Macaranga, Melastomataceae/Combretaceae*, and the shade bearer taxa *Celtis* and *Dasylepis* (Figure 3). The presence of fossil pollen of *Gilbertiodendron* type *dewevrei* is constant through time with a representation between 1% and 4% of the pollen count. Poaceae species have also a constant presence in our core site with values of less than 10% throughout. In addition, the palm *Elaeis guineense* is constant through our analysed period with values below

5%, but it then disappears from the record in the last 300 years. The ratio of shade bearers against light demanders shows low levels of fluctuation through time. The highest value is recorded towards present time indicating a slightly higher number of shade bearers than in the past (Figure 4). This coincides with an increase of pollen of *Celtis* and a decrease of *Alchornea* pollen.

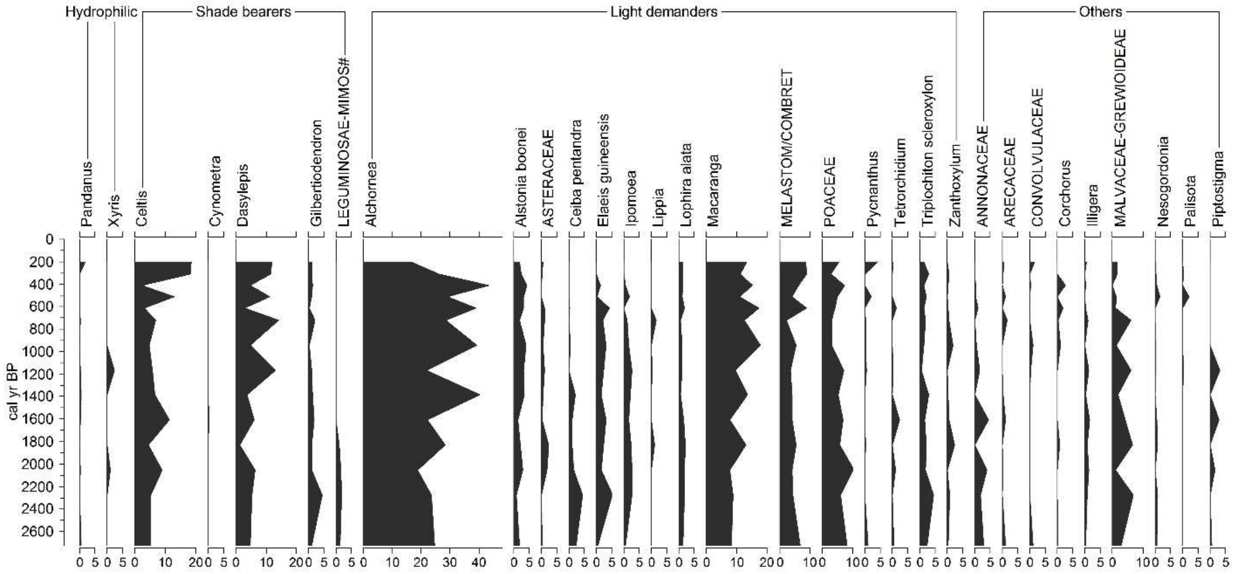

Figure 3 Pollen diagram of Core23.

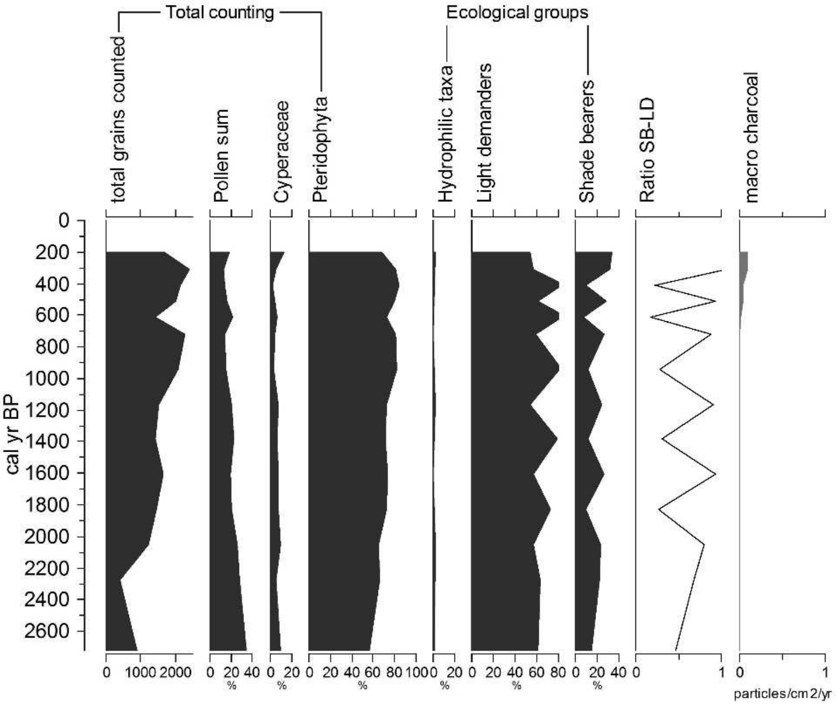

Figure 4 Summary of pollen diagram of Core23 and other proxies.

Fires, as evidenced in the fossil charcoal record were almost absent from our core site showing only a very small charcoal presence in the last 300 years with a value of 0.04 particles/cm^2/yr (Figure 4). The effect of this minimal burning on species composition was tested using a CCA, which shows that charcoal does not have any influence on species composition (p-value = 0.06).

Changes in composition and comparison with other vegetation histories in the region

In our statistical analysis using two zonation techniques for Core23, we looked for periods of distinctive vegetation composition. These analysis identifies only 1 meaningful zone with either technique (Figure 5). This indicates that vegetation mainly remained constant with little change during the last 2700 years. This result differs from those found in the other two records collected within the same region of Core23 (Sangha River). It is clear that at least 2 periods with different species composition can be identified for Goualougo and Mopo Bai (Figure 5, Figure S2 and S3).

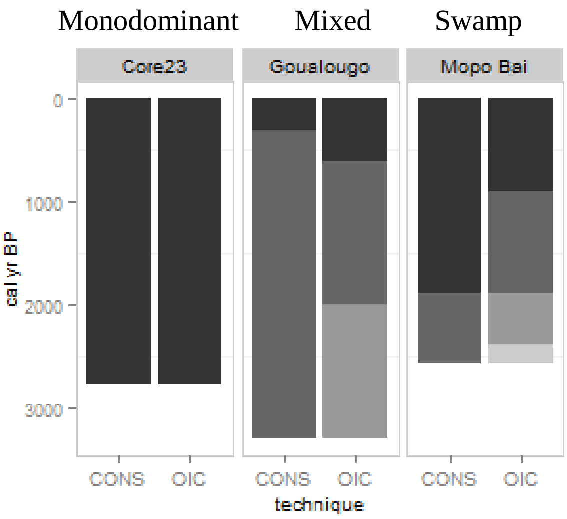

Figure 5 Zonation analysis. Optimal splitting by information content (OSI) and the CONSLINK cluster (CONS) techniques were applied to pollen data of Core23, Goualougo and Mopo Bai collected in current monodominant forest, mixed and swamp forest respectively. Different types of grey represent periods with different forest vegetation composition.

The PCA biplot shows the trajectory of change across species composition for Core23, Mopo and Goualougo (Figure 6). A gradual change in composition can be observed for Mopo Bai and Goualougo but composition for Core23 hardly changes. For example, in Mopo Bai the higher initial affinities with Poaceae and the palm *Elaeis guineense* change towards the present composition when Melastomataceae/Combretaceae are more important.

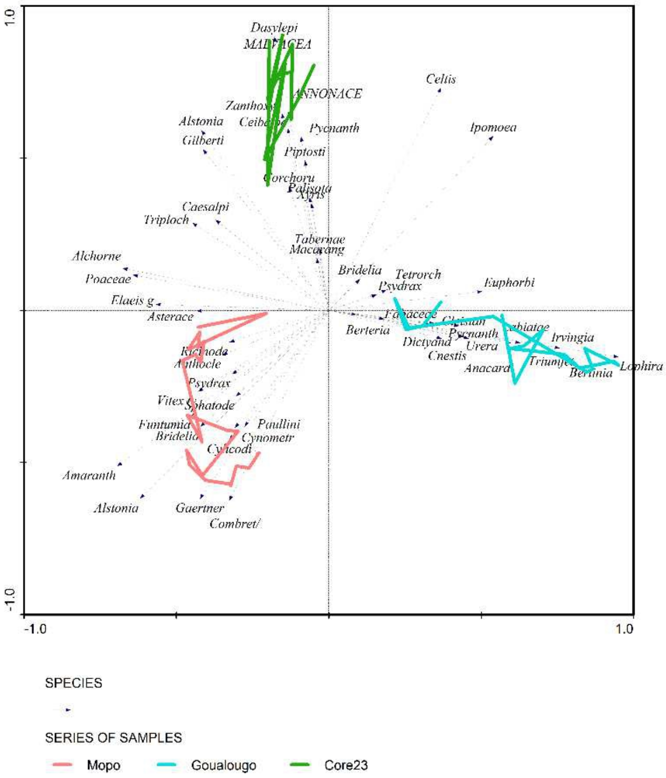

Figure 6 PCA showing the different trajectories of change of species composition over time for Core23, Goualougo and Mopo Bai (collected in current monodominant, mixed and swamp forest respectevely).

DISCUSSION

Long-term stability of monodominant *Gilbertiodendron* forest

Our results show that the monodominant forest patch we sampled has existed for the last 2700 years. Two main indicators provide evidence of the stability of this monodominant forest over time: 1) Pollen percentages of *Gilbertiodendron* type *dewevrei* in present soil surface samples are similar to those found through time as seen in the sedimentary sequence (up to 5%) and, 2) No significant statistical change in pollen composition over time is detected using two zonation techniques.

The low pollen representation of *Gilbertiodendron* in the pollen spectra contrasts with the high dominance of the species in the canopy. However, the low pollen production in the Leguminoseae-Caesalpinoideae has been documented in previous studies (Brenac 1988; Jolly *et* *al.* 1996) and the presence of even a few grains of these species can certainly indicate the presence of the species, while the absence of pollen grains does not necessarily indicate an absence of the species (Watrin *et al.* 2007). In our case we have a constant presence of *Gilbertiodendron* pollen grains, which suggests a persistence of this species over the past 2700 years. Reasons for the low production of *Gilbertiodendron* pollen may be related to the low dispersal capabilities and the low flowering frequency of the species. Bees are the main pollinator agents of this species (Ewango, personal communication) which confers a limited distribution of the pollen (Bawa *et al.* 1985). Additionally *Gilbertiodendron dewevrei* has synchronous supra-annual flowering and fruiting (Hart 1995) with flowering events occurring every 5-7 years but with occasional annual flowering of some populations (Ewango, personal communication and personal observations in our study site).

In contrast to the low representation of *Gilbertiodendron* in the sediment record, one of the most abundantly represented pollen types throughout the studied time period is *Alchornea* (16%-43% of pollen count). Nevertheless its presence is limited in our soil surface samples within the monodominant patches (<6%). *Alchornea cordifolia*, as a light demander and pioneer species with very high pollen productivity (Watrin *et al.* 2007), occurs at present day in this region especially in seasonally inundated areas in full sunlight just like the conditions at the borders of the pond (100 m diameter). Therefore the pollen of *Alchornea* is over-represented resulting from a local source.

The statistical zonation analysis does not identify a significant change in vegetation composition for the last 2700 years in Core23 site, which shows a long stability in the composition of the monodominant forest. This long-term stability contrasts with other pollen records covering the same interval of time from the same region (within 30 km) that represent mixed and swamp forest (Brncic *et al.* 2007, 2009). At these other sites (Goualougo and Mopo Bai, Figure 1) there is evidence for the vegetation being affected by climate and anthropogenic fires leading to changes in composition, thus suggesting the mixed forest and the swamp forest are less stable than the monodominant forest.

Monodominant forest and fire disturbances

Alongside stability in vegetation composition of the monodominant forest over the past 2700 years, the charcoal evidence indicates that local fires have been minimal and only in the last 300 years. Charcoal influx values are very low (< 0.05 particles/cm^2/yr) in comparison to other sites within the Sangha River region where macroscopic charcoal has also been sampled (Tovar *et al.* 2014). Two other cores collected in current monodominant forest have also shown small peaks of charcoal in the last 300 years and a complete absence of burning in the previous 2,200 years (Tovar *et al.* 2014). In one of them (site 7 shown in Figure 1) unpublished pollen data also shows the constant presence of *Gilbertiodendron* pollen for the last 2200 years (Brncic, personal communication). It is likely that these low recent local fires may have occurred in the borders of the pond where Core23 was collected as shrubs are currently observed at the border (see description of collected material) and not necessarily within the monodominant stand. All of this indicates that fires were mainly absent from the monodominant forest and that this forest may be able to cope with very low intense recent fires, most likely, localized fires nearby without any change on its composition.

Monodominant forest and climatic disturbances

The stable forest composition of the monodominant forest appears to have occurred despite apparent climatic disturbances recorded over the past 3000 years in palaeoclimatic records for this interval in time. The most important of these was a dry event that occurred between ~ 3000-2500 cal BP. For example, a decrease of precipitation is recorded in a sedimentary record collected in the mouth of the Congo river at around 3000 cal BP using hydrogen isotopic analysis (Schefuß *et al.* 2005). The impact of this event on forest composition has been detected in pollen records from the Congo basin, where in general a major decrease of mature rainforest trees is observed, but the levels of degradation were different between sites (Vincens *et al.* 1999; Bonnefille 2011). The different forest responses among pollen records to this climatic event (e.g. increase of pioneers and light demanders, conversion from forest to savannah) suggest that local factors at the sites may have played more important roles than previously thought (Willis *et al.*

2013). The occurrence of the dry event has been dated at different times between 3000 and 2500 cal BP (Vincens *et al.* 1999; Bonnefille 2011). The discrepancy in time is attributed by Ngomanda *et al.* (2009b) to uncertainties in dating and the differences in resolution of the different pollen records. The authors use a high-resolution pollen record collected in southern Cameroon to show that the climatic crisis occurred between 2500-2400 cal BP in the Congo basin. However this is still under debate.

No statistically significant change in vegetation composition is observed for Core23 throughout this dry event. One potential explanation is that the event occurred before the period covered by our core, which starts at around 2700 cal BP. Alternatively, the event may not have been strong enough to change the vegetation in this part of the Congo Region. The Goualougo record spanning 3300 cal BP does not record a major change in composition, while the Mopo Bai record did show a response to this climatic event (Figure 5), indicating the stochastic nature of vegetation response to this dry event.

After this major dry event, different periods of reduced precipitation have been identified for our study area, the Sangha River region in the Mopo Bai and the Goualougo records, based on wind-blown dust signal (Brncic *et al.* 2007, 2009) as well as elsewhere based on pollen records from the Congo basin (Bonnefille 2011). The change in vegetation composition in Goualougo and Mopo Bai between 2500-1100 cal BP (Brncic *et al.* 2007, 2009) (Figure 5) in the absence of local fires (Tovar *et al.* 2014) suggests the climate as the dominant driver of these changes. This is supported by studies in other parts of the Congo basin based on pollen composition. In Gabon, Ngomanda *et al.* (2007) attribute the change in species composition in the last 1.5 millennia solely to climatic factors as they did not record fire occurrence in their study sites. Lake Ossa and Lake Barombi in Cameroon have also shown changes in species composition of their forests which have been attributed also to climate (Giresse *et al.* 1994; Reynaud-Farrera *et al.* 1996).

Uncertainties related to the use of pollen records and wind-blown dust as proxies of climate (Willis *et al.* 2013) make it difficult to establish the precise occurrence of dry events in the Sangha

River. But if indeed several minor dry events have occurred, our results show that the monodominant *Gilbertiodendron* forest persisted indicating a level of resilience not seen in other forest types. One possible explanation for this high resilience to small dry events could be the dense and closed canopy of the monodominant forest. A close canopy may reduce soil water evaporation from the rainforest, thus reducing the effects of a dry period, but further work is needed to determine other possibly traits leading to resilience of this forest type.

CONCLUSIONS

We test the past stability of a current monodominant *Gilbertiodendron* forest in northern Congo for the last 2700 years using fossil pollen from a sediment core (Core23). Our results show that the monodominant forest currently present in the Sangha River region has existed for at least the last 2700 cal BP. The constant presence of *Gilbertiodendron* type *dewevrei* pollen throughout the studied period and the absence of any statistically significant change in species composition provide evidence for the persistence of the monodominant forest. This is in contrast with two other records from mixed forest (Goualougo) and swamp forest (Mopo Bai) located within 30 km from Core23, which show changes in vegetation composition for the same period (Brncic *et al.* 2007, 2009).

The reconstruction of past fire and climatic disturbances evidence two opposite patterns. Local fires were absent in Core23 site until 300 cal BP, when minimal burning starts to be detected. Contrary to the minimal occurrence of fire, several studies have documented both major and smaller dry climatic events during the last 2700 cal BP for Central Africa using different palaeorecords. Although most palaeorecords collected within the Congo basin exhibit changes in fossil pollen composition as a response to these dry events (see Bonnefille 2011 for a review), our Core23 does not record any major change in vegetation for the whole time series. One explanation to the lack of response to the major dry event that occurred at around 3000-2500 cal BP may be the incomplete time coverage of Core23, which starts at around 2700 cal BP.

The lack of response of the monodominant forest to the subsequent minor climatic disturbances leads to the conclusion that monodominant *Gilbertiodendron* forest exhibit long-term stability and it is also a forest type resilient to small fluctuations in climate.

Similar long-term stability in vegetation composition has been observed for Lake Bosumtwi, Ghana, outside the Congo basin in the face of climatic disturbances (Maley 1991; Miller & Gosling 2014) suggesting that this is also a resilient forest. Our Core23 is the first core within the Congo basin to indicate such a stability and resilience to minor climatic events. The location is significant given that it is well inside the present day Congo basin forest block, and that it is the first record describing the history of a monodominant forest. As such, our results contribute to showing the high landscape variability in forest responses to climatic disturbances through time within the African rainforest.

The hypothesis of long-term minimal disturbance requirement for the presence of monodominant forest (Peh *et al.* 2011a) seems to be confirmed at least for fire. There is little evidence for disturbance by fire in Core23 which would support this hypothesis. However, there clearly was climatic disturbance in this region (as evidenced in other records) but, the forest seems to have persisted despite these disturbances. Several mechanisms therefore appear to be interacting to maintain the monodominant forest (Peh *et al.* 2011a) including a persistence to climatic (dry events) disturbance. One explanation for the apparent resilience of *Gilbertiodendron* forest to climatic disturbances is that the very close canopy protects the forest from higher soil water evaporation during dry periods. Therefore, although monodominant forest show high resilience to climatic disturbances, it is likely that other disturbances that involve opening of the canopy (e.g. logging, major fires) may seriously affect its persistence.

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SUPPLEMENTARY MATERIAL

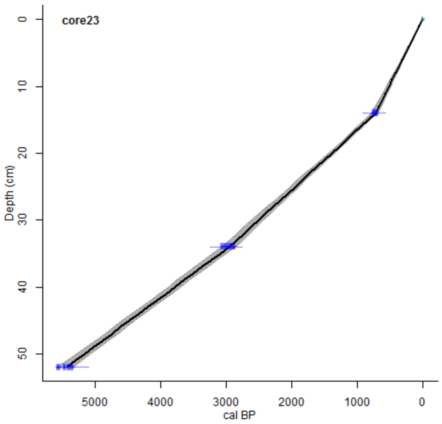

Figure S1 Age-depth model of Core23.

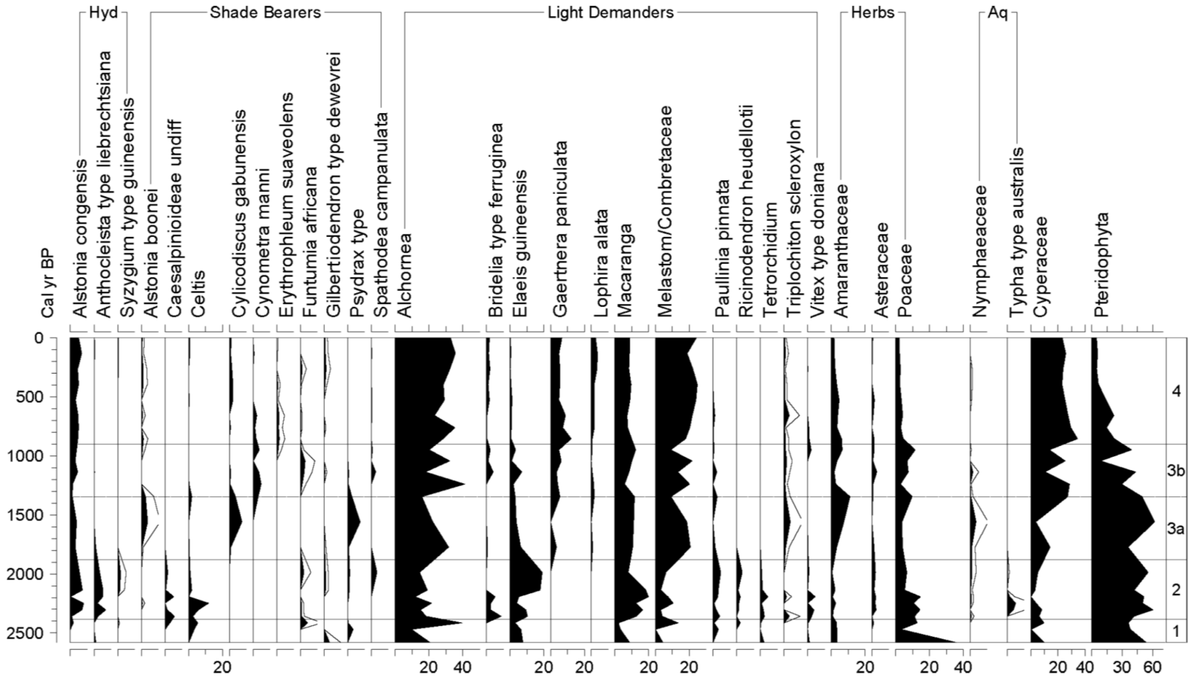

Figure S2 Pollen diagram of the Mopo Bai core collected in swamp forest (Brncic et al. 2009)

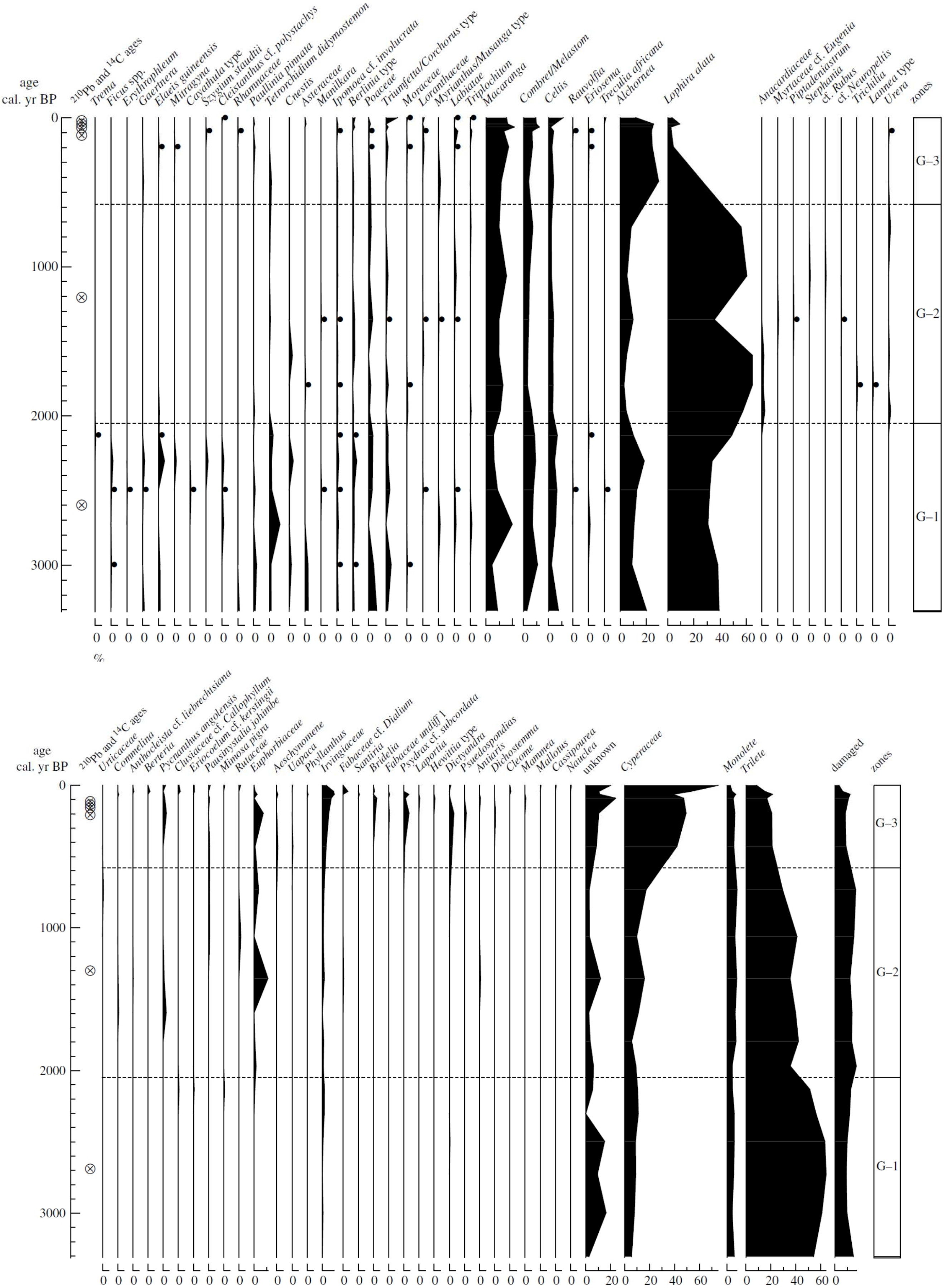

Figure S3 Pollen diagram of the Goualougo core collected in mixed forest (Brncic et al. 2007)

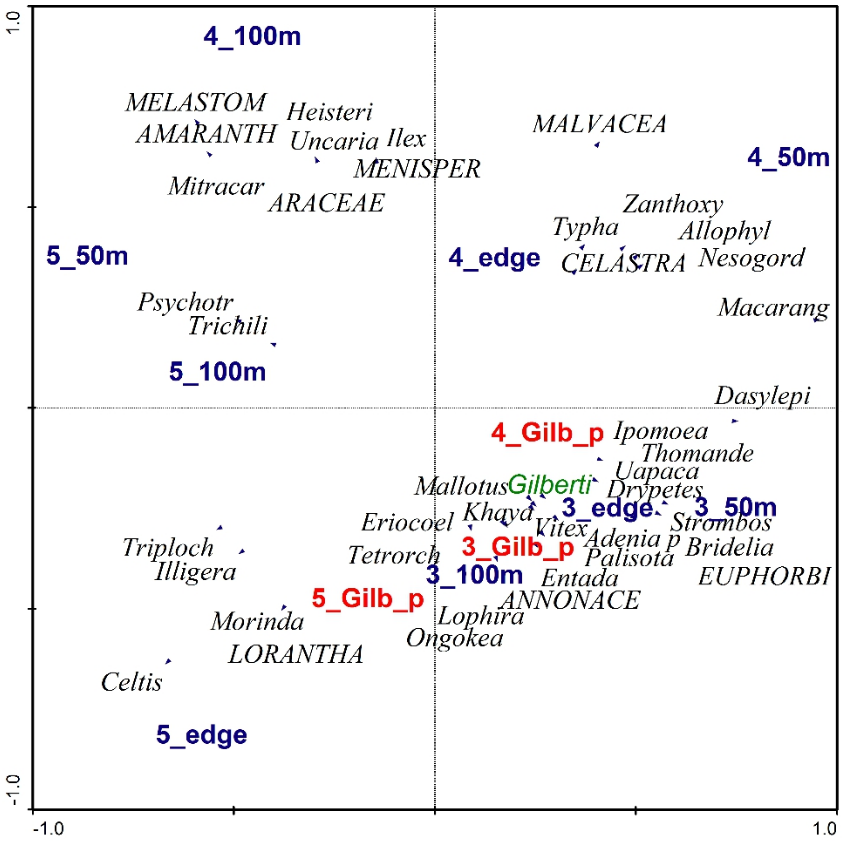

Figure S4 PCA biplot of soil surface samples. Species shown are the ones with species fit range between 10% and 100%. Samples collected within Gilbertiodendron patch are highlighted in red while the arrow corresponding to Gilbertiodendron species is shown in green.

CHAPTER 5: TESTING RAINFOREST NICHE STABILITY: CHANGES IN THE CENTRAL AFRICAN RAINFOREST DISTRIBUTION IN THE LAST 6000 YEARS

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ABSTRACT

Projections on the future extent of rainforest under climate change conditions are based on ecological niche models (ENM) that assume that the relationship between vegetation and climate has remained relatively unchanged through time (climatic niche conservatism). However, a number of recent studies have challenged this assumption. Here we test climatic niche stability of the African rainforest biome using fossil records spanning the last 6000 cal BP. We simulated rainforest distribution at 1000 year time steps using ENM and use fossil pollen records to evaluate the simulations and thus the strength of the relationship between rainforest and climatic parameters through time. Three algorithms and two sets of variables are used in the modelling. Our results show that ENM have a good fit with present day rainforest distribution, but diverging performance for the past distribution. We conclude from this study that the African rainforest may have experienced a partial shift of its climatic niche over the past 6000 years in relation to the length of the dry season. Our results suggest that the length of the dry season has become more important in determining forest distribution over time. In contrast the relationship with precipitation appears to have remained more constant for the last 6000 years. These findings make an important contribution to improving future projections of rainforest distribution under climate change scenario.

Keywords: biomisation, ecological niche models, niche conservatism, past climate change, tropical forest

INTRODUCTION

The importance of tropical rainforest has been highlighted in many different studies because of the wide range of environmental ecosystem services it provides such as carbon storage and its high biodiversity (e.g. Naidoo *et al.* 2008). Understanding the relationship between this biome and climate change therefore provides an important research challenge. A recent study that has analysed the future distribution of tropical rainforests using ecological niche models (ENM) has projected some dramatic changes (Zelazowski *et al.* 2011). These models use the observed climatic conditions in the current extent of these rainforests and assume climatic niche stability, specifically a temporally invariant relation between the vegetation and the governing climate (Araújo & Pearson 2005). However, this approach is not without its critics. For example, at species level, some recent studies have demonstrated that species may be able to change their climatic niche through time (Pearman *et al.* 2008; Peterson 2011). At a biome level for tropical rainforest, climatic niche stability remains untested.

Niche is a key concept in ecology and was defined by Hutchison as the set of abiotic and biotic characteristics that are required for the persistence of a species population through time (Hutchinson 1957). The fundamental niche represents all the abiotic characteristics required for the species persistence, while the realized niche represents the area of the fundamental niche constrained by competition with other species (Hutchinson 1981). Ecological niche models (ENN), also known as species distribution models (SDM), try to represent the niche of a species by relating observational data of the species occurrences with environmental data (Guisan *et al.* 2014). In the past few decades, the number of studies using these models to project species distributions for present and future time have experienced an exponential growth (Soberon 2007). More recently these models have also been used to project present and future distributions of biomes (Zelazowski *et al.* 2011; Tovar *et al.* 2013).

One of the main assumptions of the ENM is the stability of the niche through time or niche conservatism, which is defined as “the retention of niche-related ecological traits” (Wiens *et al.* 2010) Whether the ecological tolerances to specific climatic conditions that are displayed by the plant or animal presently are the same as those displayed through time (climatic niche conservatism) is a critical question (Wiens & Graham 2005; Wiens *et al.* 2010). Understanding climatic niche conservatism therefore has important consequences for projections of future distribution under climate change, especially in conservation schemes that develop actions based on the outputs of these models to mitigate the climate change impact on biodiversity. A recent study used paleorecords to test for niche conservatism and its effects on projections of the distribution for 3 different tree species in Europe (Maiorano *et al.* 2013). The authors demonstrated that even a certain degree of observed change in the realized niche (but not statistically significant) may have a large impact on the spatial projected future distributions of the species (Maiorano *et al.* 2013).

Recently, the African rainforest has received increasing attention because despite being the second largest forest block of the world, it is the most understudied among global rainforests (Malhi *et al.* 2013). This rainforest has a history of change in both its climate and its vegetation. For example, since the mid-Holocene (~6000 cal BP) until present time, climatic events have been observed to have a significant effect on forest composition. A number of different lines of evidence from fossil records indicate that the mid-Holocene in Africa was the wettest period of the Holocene for the Central African region (Gasse 2000; Schefuß *et al.* 2005) and that during this time rainforests expanded northwards of their current distribution (Vincens *et al.* 2010; Willis *et al.* 2013). However, a large body of evidence from fossil pollen records from Central Africa suggests that between 3000 and 2500 cal BP a major decrease in species typical of evergreen forest occurred as a result of an extended dry season. During this climatic event, some rainforest was converted into littoral grasslands or savannahs (Vincens *et al.* 1999, 2010; Bonnefille 2011). Some other areas remained forested but showed an increase in pioneer species (Elenga *et al.* 1996; Reynaud-Farrera *et al.* 1996; Maley & Brenac 1998; Brncic *et al.* 2007, 2009; Ngomanda *et al.* 2007, 2009b), while other areas changed from forest to grasslands with enclosed swampy areas (Elenga *et al.* 1994). The different rainforest responses during this time interval highlight a high spatial variability and suggest a dynamic forest-savannah mosaic where rainforest contraction was not homogeneous.

The variability in climate and vegetation composition over the past 6000 years as evidenced in the fossil records therefore provides an important opportunity to test whether the rainforest biome is affected in the same way by climatic conditions as it was in the past. In particular it enables testing of ENM based on current understanding of the climatic niche and question whether this biome have remained within similar climatic parameters (i.e. niche conservatism) or whether these have changed over the past 6000 cal BP.

In this study we aimed to use the variations apparent over the past 6000 years in response to climate change to investigate the African rainforest biome climatic niche stability. We focus on the period from mid-Holocene (~6000 cal BP) until present because it has the most number of pollen records available and the presence of distinctive climatic events. We used ENM to simulate forest distribution at a 1000 year time step and corresponding fossil pollen records to validate those simulations. Such a regional analysis using terrestrial sediments at different time steps offers possibilities to identify present and past climatic niche and the most important variables driving changes in distribution and forest ecology, leading to a better understanding of present and future risk of tropical African forest under climate change.

METHODS

Study area

The study area covers Central and West Tropical Africa (between 15°N and 15°S and < 27°E). Currently the main biomes in this area are grasslands, deciduous shrublands, deciduous forest, evergreen forest and also extensive agricultural areas (Mayaux *et al.* 2004) (Figure 1). Here we used the term “rainforest” for the humid forest (semi-deciduous and evergreen) of the Guineo-Congolian ecoregion of West and Central Africa (White 1983) as it has been used in other studies (Malhi *et al.* 2013; Hély *et al.* 2014). Within this ecoregion, the Congo domain expands from eastern Nigeria to Angola and the Guinea domain covers the northern coast of the Gulf of Guinea from Gambia to Central Nigeria (Brenan 1978). The Guinea domain is split in two by the presence of the Dahomey Gap, a corridor of savannahs (Salzmann & Hoelzmann 2005).

Biome data

Data for the present time

Rainforest presences and absences were extracted from the African land cover map for the year 2000 (Mayaux *et al.* 2004) (Figure 1). Thirty five points with forest presence were randomly selected from the land cover classes evergreen forest and swamp forest. Thirty five random forest absence points were extracted from any of the other land cover classes. Areas of savannah-forest mosaic or forest-cropland mosaic were considered neither for presence or absence as the potential vegetation under pristine land use was unknown. We extracted a set of presence and absence points to calibrate the model and another set of points to evaluate the model.

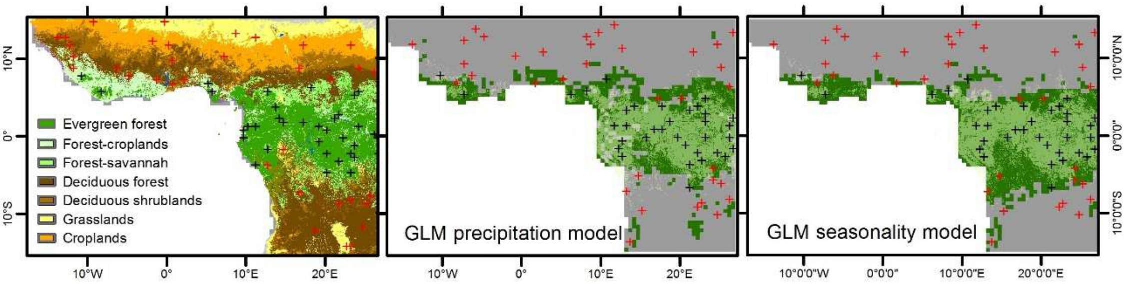

Figure 1 Study area. Left: Present biomes based on the African land cover map for 2000 (Mayaux et al. 2004). Centre and right: Simulated potential forest distribution for the present using the outputs of the GLM with the threshold that maximizes the best KAPPA value (max KAPPA) to define binary simulations for present. Black crosses represent forest presences and red crosses forest absences. Presences and absences used for model calibration are shown for the land cover map while presences and absences used for model evaluation are shown for the simulated binary maps.

Past biome reconstructions from pollen records

Pollen records were used to generate a dataset of past rainforest presence and absence for the last 6000 cal BP. The biomisation method allows the identification of the most likely biome for each pollen sample based on its pollen composition (Prentice *et al.* 1996). Each species represents one or more plant functional types (PFT) and a biome is defined by a combination of different PFT. For Africa previou studies have assigned one or more PFT to each especies (Jolly *et al.* 1998; Lebamba *et al.* 2009a). In this way, affinities of each pollen taxon for each biome are calculated based on its percentage of the pollen count (See details in Appendix S1).

We retrieved all available fossil pollen records for the study area from the fossil pollen database (http://fpd.sedoo.fr/fpd/english.do) known as the African pollen database (APD) (Vincens *et al.* 2007), excluding marine cores. Due to the coarse resolution of the paleoclimate layers (pixels size ~55km), some of the pollen records located in littoral areas were outside the paleoclimate layers extent, and were therefore excluded. The spatial analysis unit of this study is a pixel of ~55 km size, therefore, when two records were located in the same pixel we chose the core with more samples and better dating information. Data from APD were complemented with other published pollen records (Table S2). The pollen diagrams of these studies were digitized using the software Plot Digitizer v.2.6.5 to obtain the percentage values. Lastly, we also included the pollen record from Lake Barombi where the values for affinity to different biomes were already calculated following the same methods we have described before (Lebamba, Vincens & Maley 2012).

A total of 21 pollen records were collected (Table S2) and biomization values for each of them calculated (see Figure S2). The most likely biome for each record was obtained at every 1000 year time slice for the last 6000 cal BP. Then, for each time step, records indicating a forest biome were assigned as forest presence points, while records representing any other biome were assigned as forest absence points.

Environmental data

Many studies show that the current potential distribution of tropical rainforest at regional scale is mainly driven by both total annual rainfall and its seasonality (Good & Caylor 2011; Lehmann *et al.* 2011; Murphy & Bowman 2012). Other factors such as temperature, topography, soils, and fire, play a role as well, but their influence is minor compared to water availability drivers (Murphy & Bowman 2012). Based on this information and the availability of data we used a combination of paleoclimate and topographical layers in our ecological niche models.

For the paleoclimate data we used the outputs of the Hadley Centre climate model (HadCM3) (Gordon *et al.* 2000; Pope *et al.* 2000) at every 1000 year time slice for the last 6000 cal BP. Raw outputs comprised monthly mean temperature and monthly total precipitation. This model relies on a variety of abiotic variables including orbital forcing, orbital changes, greenhouse gasses and ice-sheet trends to simulate palaeoclimates at each time step (Singarayer & Valdes 2010). It should be noted that no fossil pollen records have been use to calibrate the model. The climatic simulation outputs consist of 2.5° in latitude and 3.75° in longitude resolution that were linearly downscaled to 0.5° by 0.5° pixel size (~55 km at the equator).

The final variables selected for the modelling were:

- Total annual precipitation (mm/year) indicating water availability. This variable was calculated by summing up the monthly precipitation.

- Length of dry season (number of months): This variable also indicates water availability and was calculated following (Mayaux *et al.* 2005). A dry month was defined when total rainfall (mm) was lower than twice the mean temperature (°C). Units are number of months.

- Mean annual temperature (°C): This variable has shown to be important in dynamic vegetation models used to project rainforest distribution (Delire, Ngomanda & Jolly 2008). It was calculated by averaging all mean monthly temperatures.

- Soil water holding capacity (mm m^{-1}): This is another important variable accounting for water availability and was obtained from the Global Digital Soil Map (Food and Agriculture Organization 1995). It represents the water holding capacity of the soil at 30 cm depth.

- Topographical complexity: This is a proxy for fire spread, as more topographically complex areas are less prone to large fires (Lehmann *et al.* 2011) and it also has been related to soil water availability (Murphy & Bowman 2012). Following Lehmann *et al.* (2011), we calculated the standard deviation of 30s arc-degree resolution of elevation (Lehner, Verdin & Jarvis 2006) within a 0.5 arc-degree pixel size.

Since total annual precipitation and length of dry season were highly correlated (Figure S1) we created two sets of variables to avoid co-linearity. Each set had one of the two correlated variables and all the rest of the variables. For the rest of the paper we refer to these two sets of variables as precipitation models and seasonality models.

Ecological niche modelling

We used BIOMOD2 to model the present rainforest distribution using an ecological niche model approach (Thuiller *et al.* 2009). The presence or absence of forest for the present was related to the two sets of environmental variables (precipitation and seasonality) by using three different statistical algorithms: logistic regression (GLM), random forest (RF) and generalised boosted models (GBM). Model parameters are described in Table S1. This results in 6 different models (3 algorithms x 2 sets of variables): three precipitation models and three seasonality models. All model output maps were scaled between 0 and 1000 using a binomial GLM in BIOMOD2 to enable comparison of all the algorithms used.

Each of the six models was calibrated with the same set of randomly selected forest presence and absence points and then evaluated against a second set of randomly selected points using three different metrics of overall performance: Cohen's kappa index (max KAPPA), the maximum true skill statistic (max TSS) and the area under the ROC curve (AUC) (Liu, White & Newell 2011). Performance values closer to 1 indicate better performance while values closer to 0 indicate a model that is not better than a random model.

All models were used to simulate forest occurrence for the current and past climate (7 time steps at every 1000 years). The outputs of each model are probabilistic maps with values between 0 and 1000, where 1000 indicates the highest probability of forest presence. Binary maps (presence/absence maps) were created from the probabilistic outputs of the simulations by using three different thresholds: threshold values obtained by the max KAPPA, max TSS and the best threshold extracted from ROC plot. These metrics in general select a threshold at which the final binary map represents better the presences and absences from the evaluation points (Liu *et al.* 2005). The binary maps of past rainforest distribution, obtained with the three different thresholds mentioned above, were evaluated against past rainforest biome presence/absence reconstructed from fossil pollen records (see biome data section) using the TSS metric. The TSS was chosen because it accounts for prevalence, which makes it stronger than KAPPA (Allouche, Tsoar & Kadmon 2006).

BIOMOD2 also allows for relative importance ranking of the explanatory variables (Thuiller *et al.* 2009). This involves the calculation of Pearson correlation between the fitted values of the full model and fitted values of a model where the variable to be evaluated has been randomly permutated. Lower values of correlation indicate higher contribution. BIOMOD2 then uses these values to make the ranking by scaling them between 0 and 1, where values closer to 1 indicate a higher contribution to the model.

Environmental niche based on paleodata and present data

In order to have a representation of the climatic niche space we used the biplot of the principal component analysis (PCA) of the climatic variables. For this, we extracted the values of all environmental variables at each time step from the location of each forest presence (fossil pollen data and calibration data for present) to perform the PCA (Maiorano *et al.* 2013). We performed a second PCA, including again the values of environmental variables at the site of pollen records collection and environmental variable values of all rainforest pixels from the land cover map of Mayaux *et al.* 2004 to fully describe the present niche. PCA biplot was also produced for this second analysis.

Changes in rainforest extent and distribution

We selected the models with the highest performance values to analyse the changes in rainforest distribution for the last 6000 cal BP. First, maps of changes in rainforest distribution between 1000 year time intervals 6,000-5000 cal BP and so on until present time were prepared to show the areas that remain unchanged, the areas of forest that were lost during the analysed period, and areas where new rainforest areas appeared by the end of the analysed period. Next, we calculated the percentage of overall change for each time step in comparison to the simulated current rainforest area:

$$\%change = \frac{F_{ti} - F_{t0}}{F_{t0}} \times 100$$

where F_{ti} represents the rainforest area at each time step and F_{t0} represents the rainforest area at the present time based on the model simulation onto the present climate.

RESULTS

Model simulations for present time

All models show similarly good performance suggesting that both sets of variables (precipitation models and seasonality models) represent well the current rainforest distribution (Figure S3). Values of max TSS and max KAPPA are between 0.63 and 0.77 for all six models. The RF precipitation model performs best. The values for the AUC metric range between 0.91 and 0.95 and are similar between precipitation and seasonality models (Figure S3) indicating high model performances. As expected, the variable importance assessment shows that the total annual precipitation is the most important variable in the precipitation models, while the other variables have little contribution, especially mean annual temperature (Table 1). For the seasonality models, the length of the dry season has the highest importance value (Table 1).

An example of model output is shown in Figure 1 using GLM precipitation and GLM seasonality simulations for present time. Some areas of over-prediction of rainforest occurrence at the northern and southern borders of the current rainforest area are notable. However, most of the areas of over-prediction are covered currently with forest-savannah in the Congolian region or forest-cropland in the Guinean region. These are areas that may potentially be rainforest in the absence of human activity. The main obvious feature of over-prediction occurs in the Dahomey Gap, south of Benin and Togo, which is currently a grassland corridor that divides the rainforest of the Guinean domain.

Table 1Variable importance for each model of total annual precipitation (pptot), mean annual temperature (tmean), topographical complexity (topo_comp) and water holding capacity (whc_1)

	Precipitation models				Seasonality models			
	pptot	tmean	topo_comp	whc_1	lengdrys	tmean	topo_comp	whc_1
GBM	0.957	0	0.024	0.002	0.928	0.001	0.031	0.002
GLM	0.978	0	0.138	0.098	0.939	0	0.081	0
RF	0.939	0.021	0.062	0.008	0.86	0.032	0.049	0.005

Model simulations for past times

In contrast to simulations of present rainforest distribution, simulations of past distribution using the models calibrated with present time data have different levels of performance, from models that were not better than random (TSS values close to 0) to models with high performance (TSS values close to 1) (Figure 2). For example, for the time steps between 6000 and 4000 cal BP, the precipitation models seem to perform much better than the seasonality models. While two precipitation models (GBM and RF) show TSS values above 0.5 and in some cases closer to 1, GBM and RF seasonality models have TSS values equal to 0.5 and below this value. The lowest TSS value (closer to 0) is recorded for the time step of 6000 cal BP indicating no better performance than a random model. The time steps of 5000 and 4000 cal BP are better represented by RF precipitation models (TSS values of 1). GLM precipitation and seasonality models show more similar TSS values for the time steps 6000 and 4000 cal BP.

Figure 2 Evaluation of the simulations of the past forest distribution using fossil pollen records. TSS values for binary maps produced by using best thresholds according to max KAPPA, ROC and max TSS.

For the time steps between 3000 and 1000 cal BP differences between precipitation and seasonality models are less marked than for the previous time steps (Figure 2). While GBM and

RF for precipitation and seasonality models show TSS values around 0.5, GLM models had TSS values between 0.5 and 0.9, and GLM precipitation models were the models better representing forest distribution for the time steps between 3000 and 1000 cal BP.

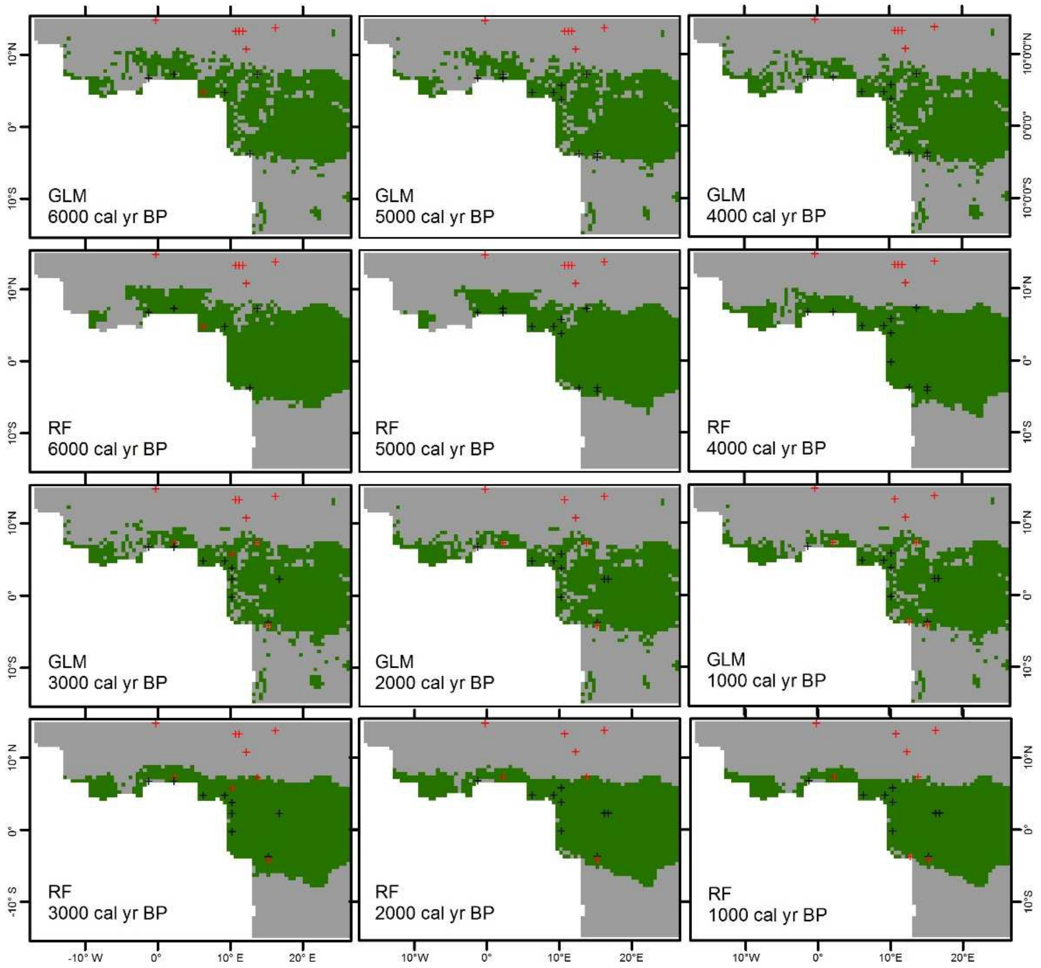

Figure 3 Simulated rainforest distribution for the last 6000 years for GLM and RF precipitation models. Binary maps were produced using the threshold determined by the max KAPPA. Black crosses indicate forest presences while red crosses represent absences based on pollen records.

To analise the spatial changes of the simulations we choose the binary maps with the best performance based on TSS metric (Figure 2). According to this metric, binary maps created using the threshold of the max KAPPA perform similarly than those using the threshold of max TSS and perform mostly better than that of ROC. Therefore we used the binary outputs created based on the threshold of max Kappa (Figure 3 and Figure 4). Here, marked differences can be observed between precipitation and seasonality models for the time steps between 6000 until 4000 cal BP. While the precipitation models show a northward expansion of the northern forest border for this period in comparison to present time (Figure 3), the seasonality models show a southward displacement of the whole forest block from the Congolian region (Figure 4). Additionally, all simulations of past forest distribution using seasonality models (all algorithms and time steps) show a smaller rainforest area in comparison with present day rainforest area (Figure 5). For example, for the time step 6000 cal BP, the rainforest area is between 9% and 17% smaller than the current forest area depending on the algorithm used. In contrast, the precipitation models show a larger forest area in comparison to the present for time steps between 6000-4000 cal BP when using GLM and RF, but a slight smaller area (by around 2.5%) for GBM (Figure 5).

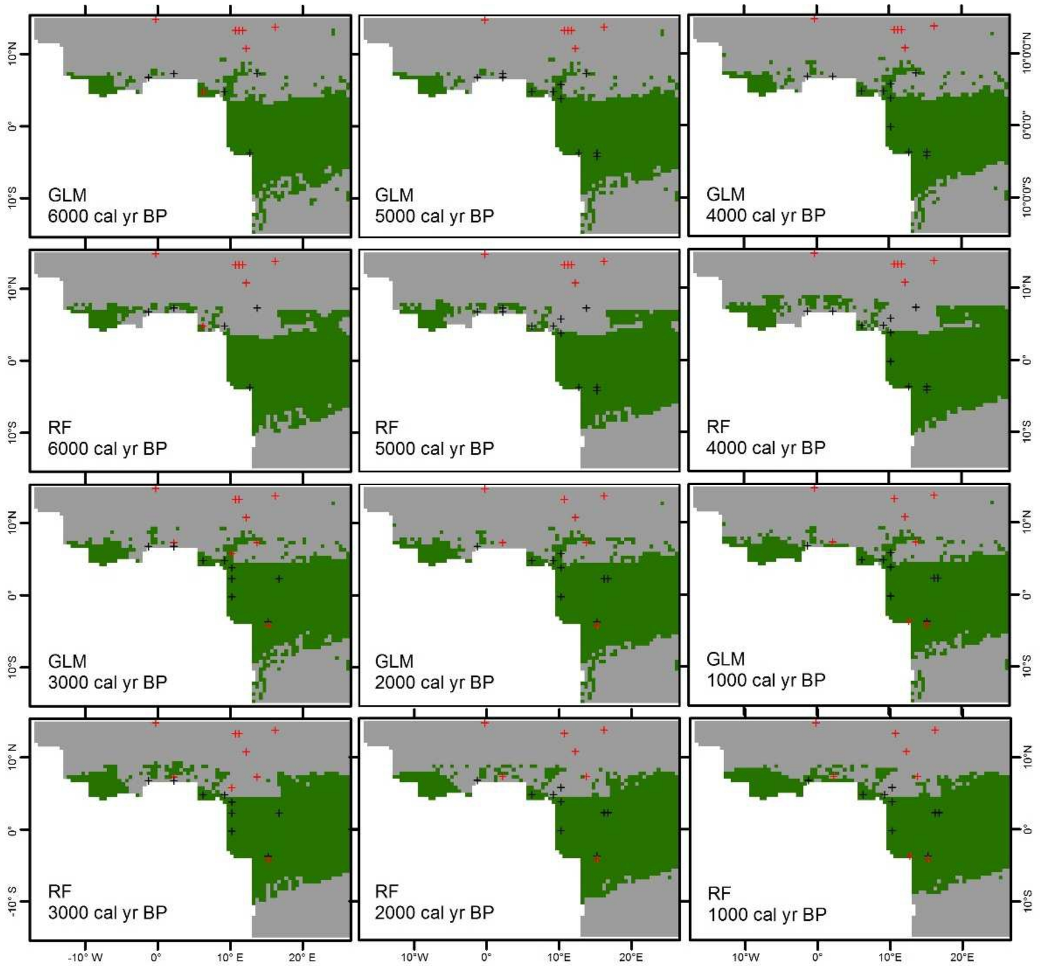

Figure 4 Rainforest distribution for the last 6000 years for GLM and RF seasonality models. Binary maps were produced using the threshold determined by the max KAPPA. Black crosses indicate forest presences while red crosses represent absences based on pollen records.

Climatic niche based on paleodata and present data

The climatic niche space of the rainforest was summarized in a biplot of the first two axis of a PCA (Figure 6). These two axes account for 64.6% of the total variability in climate over all time steps. For the precipitation vector, present rainforest samples that were used to calibrate the models are well distributed along the entire gradient, indicating that current rainforest associated precipitation represents well past precipitation regimes as well. For the vector of the length of the dry season, present rainforest samples are mostly located towards the projected base of the vector, indicating association with lowest number of months. Fewer number of present day samples are located in the area towards a higher number of months of dry season, in contrast to what is observed for samples of rainforest at 6000 and 5000 cal BP which are specially linked with a higher number of months of dry season.

A second biplot explores the same climatic niche space shown in Figure 6 but in this case, samples for present time are represented for all rainforest pixels from the land cover map, showing the whole environmental spectra for the present time (Figure S4). The first two axis account for 78% of the variability and we observe a similar pattern for the vector of the length of the dry season to the pattern observed for the first biplot. The main core of samples for present time represent low and intermediate values of number of months of dry season, and few are located in the area relating to a longer dry season. Data points of present day sample relating to precipitation are well distributed along the gradient again.

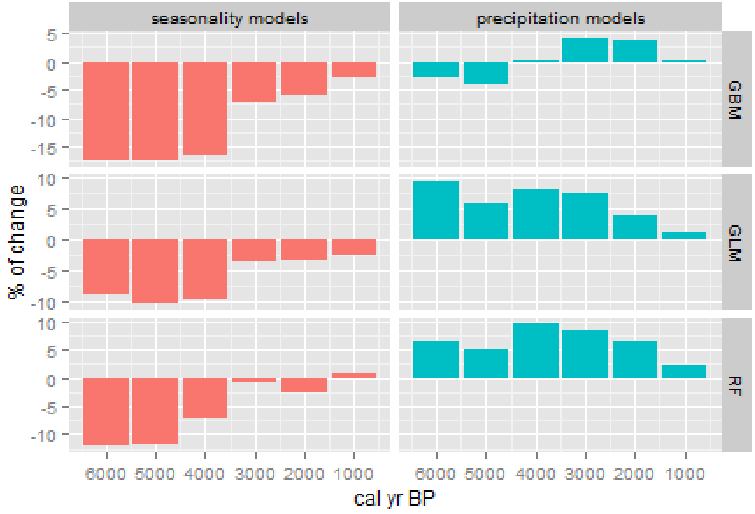

Figure 5 Percentage of change in rainforest area in comparison to simulated present extent.

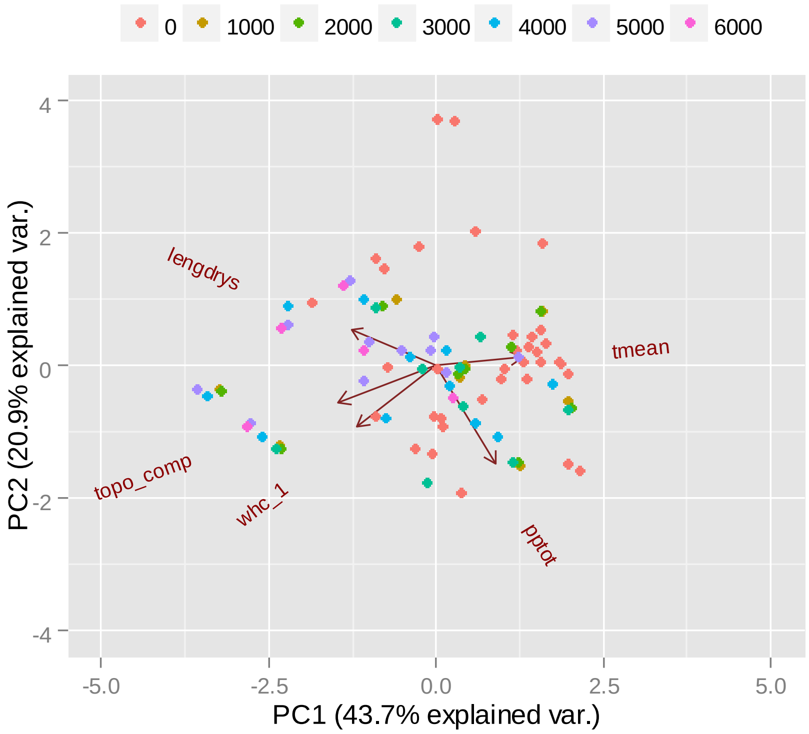

Figure 6 PCA biplot of environmental data for all rainforest presence data from the present and fossil pollen records. Different colours represent different time steps. Variables included in the analysis: total annual mean precipitation (pptot); length of dry season (lengdrys); mean annual temperature (tmean); topographical complexity (topo_comp); and water holding capacity (whc_1).

Main rainforest spatial patterns and changes

Given that the RF and GLM precipitation models have the best performance for past rainforest simulations, we describe the main distribution patterns and their changes using the binary outputs of this set of models (Figure 3 and Figure 7). The simulations indicate that for the mid-Holocene (6000 cal BP) the rainforest area reach between 8°N latitude in Cameroon and Central African Republic and 10.5°N in Ghana, Togo and Benin while the south border is located at around 5°S (Figure 3). During this time step the Guinean forest of West Africa is smaller than today, limited to Sierra Leone and Liberia, and isolated from the rest of the rainforest block, which expands from Ghana to Democratic Republic of Congo. The main difference between RF and GLM models is the degree of fragmentation of the rainforest. GLM simulations show a rainforest with some patches of non-forest within the main rainforest block especially in the Congolian domain. In contrast, RF models simulates a solid rainforest block. These patterns persist for all time steps.

As we move through the time series, after the time step of 6000 cal BP, the northern border retreats further south for GLM and RF models (Figure 7). Interestingly, the Guinean forest region has its maximum expansion for the time steps 5000-4000 cal BP together with a southward expansion of the south forest border that lasted until 3000 cal BP. Some level of rainforest fragmentation is observed for the GLM model for the period 4000-3000 cal BP, where a slight opening of the rainforest is observed in the core area of the Congolian domain. Between 3000 and 2000 cal BP, the northern and southern borders retreat, reducing rainforest area in the Congolian domain, but there is an expansion of rainforest at the northern border for the Guinean region.

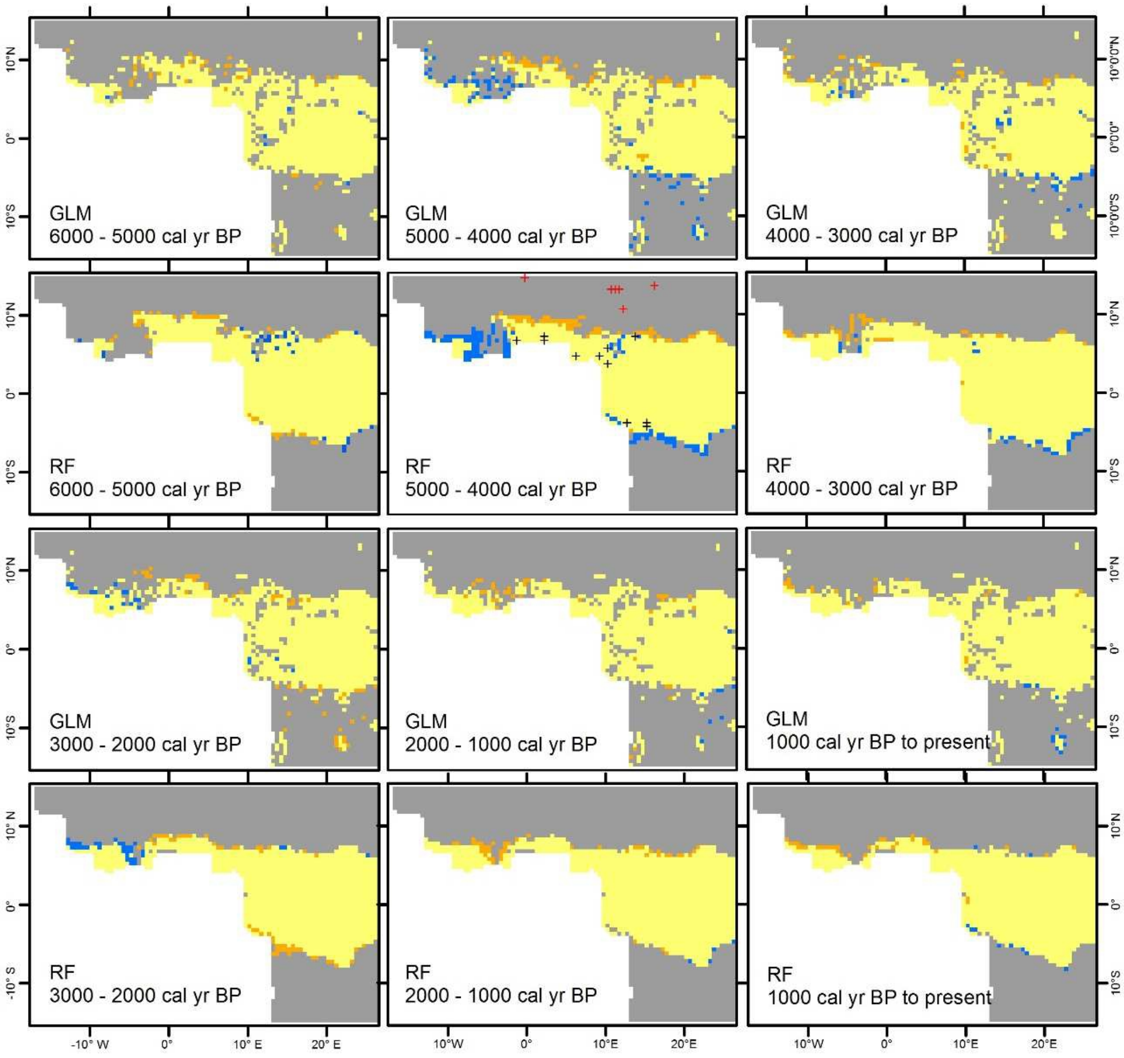

Figure 7 Changes in rainforest distribution using binary maps produced by GLM and RF precipitation models. In yellow areas that remain without change, in orange lost rainforest areas and in blue new rainforest areas for each period.

DISCUSSION

Rainforest climatic niche stability

Water availability is the most important driver of current global rainforest presence. Different proxies have been used to describe this better, such as the total annual precipitation, the length of the dry season, the dry season soil saturation, among others (Zelazowski *et al.* 2011; Hirota *et al.* 2011; Murphy & Bowman 2012). Our results show that current African rainforest distribution can be explained either by precipitation or by the length of dry season, though both of them are highly correlated. We developed models using these variables separately in conjunction with other variables (precipitation and seasonality models) showing that both sets of models perform well when describing present day rainforest distribution in Africa. Thus, for each set of models, precipitation and the length of dry season override the effect of the other variables included in our analysis.

Our results also show that the importance of these two variables may have changed through time since the mid-Holocene (6000 cal BP) until present time. Particularly for the period between 6000-4000 cal BP, the precipitation models simulated rainforest extent (as evidence from the fossil pollen record) much better than the seasonality models. A potential explanation for the poor performance of seasonality models is that non-analogous conditions occurred in the past, and therefore, the model is out of its calibration range (non-analogous climate) (Nogués-Bravo 2009). In fact, the PCA bi-plots show that all rainforest sites during this time period probably experienced a longer dry season than the present rainforest sites in combination to total annual high precipitation. This combination of climatic parameters does not currently occur in present time in areas where rainforest is present. Therefore, the African rainforest niche was less constrained in the past by the length of dry season, especially at 6000 cal BP.

The occurrence of rainforest in this particular combination of climatic parameters may be related to soil water availability. The mid-Holocene (6000 cal BP) has been reported as the wettest period of the Holocene for Central Africa (Gasse 2000; Schefuß *et al.* 2005). Paleoclimate proxies, independent from pollen proxies, suggest that an increase in local wet season intensity was driving hydrology rather than the length of the wet season (Collins *et al.* 2013). The importance of long roots, common in tropical trees, in obtaining water during the dry season has also been highlighted (Kleidon & Heimann 2000). Therefore, in a scenario of increased precipitation intensity, water availability in soils may have increased considerably too, allowing trees to obtain water through their roots even in areas with a longer dry season than present, thus reducing the impact of seasonality. Another potential explanation is the role played by cloud cover. Areas with high cloud cover may provide enough atmospheric humidity for rainforest to exist in areas with longer dry seasons or drier rainfall regimes (Lebamba *et al.* 2009a; b; Zelazowski *et al.* 2011).

From the 3000 cal BP time step onwards, the high accuracy of rainforest simulations of both models calibrated with precipitation and length of dry season suggests an equal importance of seasonality and precipitation in defining rainforest distribution. These results are in agreement with Vincens *et al.*(2010), who highlight the importance of seasonality in relation to a change from rainforest to savannah in a site located in Cameroon, 100 km north from the present rainforest northern border. The replacement of rainforest by savannah at 3000 cal BP was deduced from the pollen composition and seems to be linked to a decrease in precipitation as well as a longer dry season.

Although other drivers have been described as important for determining rainforest distribution, at a continental scale water availability is still the most important driver, not only for present time (Murphy & Bowman 2012) but also for the past rainforest distribution. However, we also found that precipitation seems to represent better water availability during the last 6000 cal BP compared to seasonality, since the same levels of precipitation to define rainforest distribution are observed for present and past times. On the other hand, few rainforest sites at present time have a length of the dry season comparable to that the palaoeclimatic models simulate for 6000 cal BP (Figure 6). Rather than a complete change in length of dry season in comparison to present time, most values of this variable at 6000 cal BP represent marginal values of the present climatic niche. Therefore we suggest that a partial shift in rainforest climatic niche has occurred with rainforest showing small changes in tolerance for length of dry season but no changes in its requirements of total annual precipitation.

More important than documenting the partial shift in climatic niche itself (Wiens & Graham 2005) is that little changes can have large impact in the geographic projections (Maiorano *et al.* 2013). Our results show that seasonality models failed entirely to simulate forest distribution between 6000-4000 al yr BP. Especially for the 6000 cal BP time step (Figure 4) seasonality models simulate a limited rainforest presence between ~5°N and ~10°N rather than the large rainforest areas documented in many different fossil pollen studies (e.g. Salzmann & Hoelzmann 2005; Vincens *et al.* 2010). Therefore, the use of precipitation as proxy for water availability should be preferable when projecting future distribution under climate change, as the relation between rainforest and precipitation seems more conservative through time.

Uncertainties in our approach are linked to the coarse resolution of the paleoclimate layers but also with the sampling of presences of rainforest in the current landscape. By using only non-human areas for calibration and evaluation of our models, we may not have captured the whole climatic niche for the present time, which is a caveat of correlative models (Soberon 2007). Further research is needed to explore whether the same patterns we found for African rainforests are observed in other rainforests. Studies have shown that the rainforest climatic niche currently differs between continents, showing that a higher level of precipitation is required for Africa than for the Neotropics (Zelazowski *et al.* 2011; Murphy & Bowman 2012). In the same way we show here that a partial temporal niche shift has occurred for African rainforest, with large consequences in the geographical simulations.

Major changes in rainforest distribution since the mid-Holocene

Our models and simulations represent the potential rainforest distribution including areas that are currently under human land use pressure, therefore over-prediction is expected in relation to current rainforest areas, especially in areas that are currently a mosaic of rainforest and savannah or rainforest and croplands (Figure 1). The main over-prediction occurs for the Dahomey Gap, a savannah corridor located in Togo and Benin that divides the Guinean region. Its presence has been associated with reduced annual precipitation values (maximum around 1000 mm) as a result of cooler surface waters, seasonal coastal upwelling during the summer and a reduced convergence (Dupont & Weinelt 1996). Marine and terrestrial pollen records suggest that the Dahomey Gap was covered by rainforest during the early and mid-Holocene and that the savannah corridor established around 4500-3400 cal BP (Dupont & Weinelt 1996; Salzmann & Hoelzmann 2005). Our simulations suggest a level of replacement of the forest with savannah in the Dahomey Gap for the period 5000-4000 cal BP. Even though the rainforest gradually reduces after this time, our models fail to simulate its complete disappearance.

Fragmentation of rainforest was observed for the beginning of the late Holocene (4000-3000 cal BP), but only for the GLM precipitation model. This model does not simulate a massive fragmentation but rather localized fragmentation. However, it is possible that using paleoclimate layers with higher resolution we could observe a more intense fragmentation process for this period as has been suggested by other studies (Vincens *et al.* 1999; Bonnefille 2011). An unexpected result is the two opposite fragmentation states produced by the GLM and RF precipitation models. The GLM precipitation models simulate a rainforest that has shown a certain degree of fragmentation since the mid-Holocene, contrary to the RF models that simulate a solid rainforest block, especially for the Congolian region. Performance of the GLM model is the highest for the period 3000 -1000 cal BP suggesting that it represents this period well, however, its performance is reduced during earlier time steps. More pollen records are needed to test which model represents most realistically the change in rainforest extent through time.

The rainforest distribution of the Guinean region is also striking, as it is only present for Liberia during the mid-Holocene. The only marine record for that region reconstructs wet conditions and suggests rainforest presence covering the coast from Guinea to Liberia at that time (Collins *et al.* 2011). Two other terrestrial records exist for the Guinean region. One, from the Ivory Coast, confirms that this area hosted rainforest for the last 6000 years (Fredoux 1983 cited by Shanahan *et al.* 2015), and the other from lake Bosumtwi in Ghana shows humid conditions for the mid-

Holocene, after which a gradual transition to drier conditions was interrupted by increased precipitation between 5,400 and 3,100 cal BP (Shanahan *et al.* 2015). Our models capture this last humid phase, showing an increase of rainforest cover for the period 5000-4000 cal BP. However, Shanahan and colleagues highlight that the paleoclimate of the Guinean region does not represent well the variability in precipitation for this region between 8000 to 2500 cal BP, which may explain the under-representation of rainforest for this area in our models.

Better paleoclimate layers for Africa will definitively improve our models and simulations, but it is also necessary to incorporate a proxy for human presence as a continuous spatial layer to account for the effect that humans had in the African rainforest. Future work should be directed to improving these datasets.

CONCLUSIONS

Analysis of the current rainforest climatic niche highlights the importance of precipitation and the length of dry season (two highly correlated variables) to define rainforest presence. It has been shown that climatic niche varies geographically with Neotropical rainforest having the most distinctive conditions among the other rainforests of Africa, Asia and Australia. Our analysis of the African rainforest for the last 6000 cal BP demonstrates that the rainforest climatic niche may vary not only spatially but also temporally. Here we test whether models calibrated with present day data of the rainforest climatic conditions would represent well past rainforest distribution. While models that used total annual precipitation (precipitation models) show good performance in representing past rainforest distribution, models that used the length of the dry season (seasonality models) fail in representing the distribution between 6000 and 4000 cal BP. During this latter period, pollen records show rainforest was present between 5°N and 10°N which is not recorded in the seasonality models suggesting that seasonality may have only played a secondary role during that period.

The analysis of the climatic niche represented by a PCA biplot that includes the climatic conditions of each of the fossil pollen records and those of the samples from present time, show that the niche does not necessarily change completely from 6000 cal BP to present. Rather, it shows a shift of the mean values of the length of the dry season towards marginal values of the current climatic niche. We suggest that African rainforest biome has suffered a partial shift of its climatic niche as length of dry season has commonly higher values in the past than at present time but precipitation remains conservative.

While some spatial patterns of rainforest change can be observed using models that included precipitation, better paleoclimatic layers at higher resolution and more fossil pollen records are necessary to improve representation of forest changes. Finally, our analysis lacks a proxy for human presence. But to date no data exist as a continuous spatial layer for this information at 1000 yr time steps. We provide evidence that models that perform well at the present time may not represent past conditions accurately, therefore it is important to take this past information into account when projections for the future effects of climate change on African rainforest are proposed.

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SUPPLEMENTARY MATERIAL

Appendix S1 Biomisation method (Prentice *et al.* 1996)

Each species is representative of one or more plant functional types (PFT) and each biome is defined based on a combination of certain PFT. Affinities of each pollen taxa for each biome are calculated based on its percentage of the pollen sum. This method has been applied before to present sample records from Africa and the reconstructed and current biome show a good correlation (Jolly *et al.* 1998; Lebamba *et al.* 2009a). Marshy or aquatic herbs and shrubs, typical swamp trees, anthropogenic taxa and all Pteridophyta were excluded from the pollen sum to calculate the percentages following Lebamba *et al.* (2009a). Species were extracted from Table 1 in Lebamba *et al.* (2009a) to identify the key taxa defining plant functional types. A list of species was made from the African pollen database (Vincens *et al.* 2007) and standardized with the names of the table from Lebamba *et al.* (2009a). We only included samples were total pollen count was at least 100 grains. PFT were assigned for each taxon following Lebamba *et al.* (2009a, 2012). If a taxon from APD was not in any of Lebamba's publications, we assigned it with the higher taxon where possible (e.g. *Cassia*-type *occidentalis* was assigned to the *Cassia* type).

Biome affinities for each sample of each pollen record were calculated for the following biomes: rainforest, seasonal forest, savannah and desert. The definition we used of rainforest (see study area section) encompasses the biomes of rainforest and seasonal forest. A continuous plotting of this affinity enabled the reconstruction of biome changes through time rather that snapshot views (Lebamba *et al.* 2012).

Table S 1 Model parameters used for each algorithm

```
-=-=-=-=-=-=-=-=-=-=-=-=-=--=-=-= 'BIOMOD.Model.Options' -=-=-=-=-=-=-=-=-=-=-=-=-=-=-=
GLM = list(type = 'quadratic', interaction.level = 0, myFormula = NULL, test = 'AIC', family =
    binomial(link = 'logit'), mustart = 0.5,
 control = glm.control(epsilon = 1e-08, maxit = 50, trace = FALSE)),
GBM = list( distribution = 'bernoulli', n.trees = 100,
 interaction.depth = 3, n.minobsinnode = 5,
 shrinkage = 0.005, bag.fraction = 0.5, train.fraction = 1,
 cv.folds = 3, keep.data = FALSE, verbose = FALSE,
 perf.method = 'cv'),
RF = list( do.classif = TRUE, ntree = 100, mtry = 'default',
 nodesize = 5, maxnodes = NULL),
```

Table S2 Pollen records used for the present study

Site name	Latitude	Longitude	Country	Reference
Lake Bosumtwi	6.5000	-1.4500	Ghana	(Maley 1991)
Lake Sele	7.1500	2.4333	Benin	(Salzmann & Hoelzmann 2005)
Yeviende	6.5350	2.3783	Benin	(Tossou *et al.* 2008)
Oursi	14.6547	-0.4878	Burkina Faso	(Ballouche & Neumann 1995)
Tjeri	13.7333	16.5000	Chad	(Maley 1981)
Bal Lake	13.3069	10.9494	Nigeria	(Salzmann 1998)
Eastern Niger Delta	4.5189	6.0763	Nigeria	(Sowunmi 1981)
Kaigama	13.2517	11.5681	Nigeria	(Salzmann 1998)
Kajemarum Oasis	13.3050	11.0289	Nigeria	(Salzmann 1998)
Lake Tilla	10.5333	12.1333	Nigeria	(Salzmann 2000; Salzmann, Hoelzmann & Morczinek 2002)
Lake Ossa	3.8014	10.0125	Cameroon	(Reynaud-Farrera *et al.* 1996)
Lake Bambili	5.9300	10.2300	Cameroon	(Lézine *et al.* 2013)
Lake Mbalang	7.3215	13.7385	Cameroon	(Vincens *et al.* 2010)
Lake Barombi Mbo	4.6627	9.3893	Cameroon	(Lebamba *et al.* 2012)
Lake Nguene	-0.2000	10.4666	Gabon	(Ngomanda *et al.* 2009a)
Nyabessan	2.3908	10.3555	Gabon	(Ngomanda *et al.* 2009b)
Goualougo	2.1637	16.5096	Republic of Congo	(Brncic *et al.* 2007)
Mopo Bai	2.2325	16.2624	Republic of Congo	(Brncic *et al.* 2009)
Bilanko	-3.5167	15.3503	Republic of Congo	(Elenga 1992)
Ngamakala pond	-4.075	15.3833	Republic of Congo	(Elenga *et al.* 1994)
Lake Sinnda	-3.8361	12.8000	Republic of Congo	(Vincens *et al.* 1998)

Figure S1 Correlation between climatic variables for present time. Variables included in the analysis: total annual mean precipitation (pptot); length of the dry season (lengdrys); mean annual temperature (tmean); topographical complexity (topo_comp); and water holding capacity (whc_1).

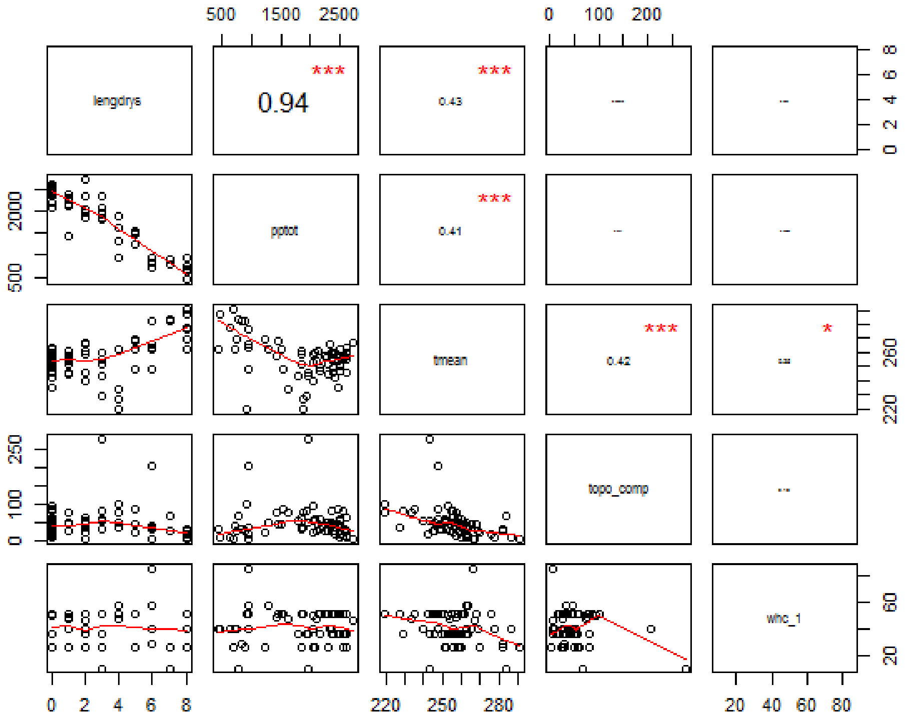


Figure S2 Biomization method applied for each pollen record. Affinity scores to each biome. Definition of rainforest (see study area section) is a combination of rainforest and seasonal forest biomes. Areas in dark grey represent periods of lake desiccation.

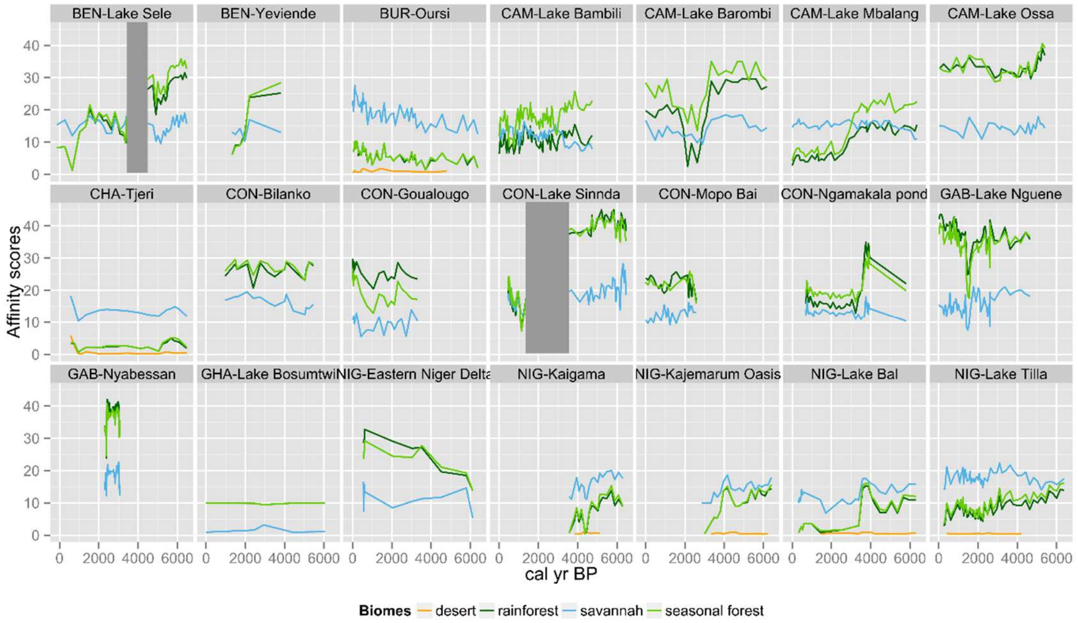


Figure S3 Evaluation for precipitation and seasonality models. Algorithms are generalized boosted models (GBM), logistic regression (GLM) and random forest (RF)

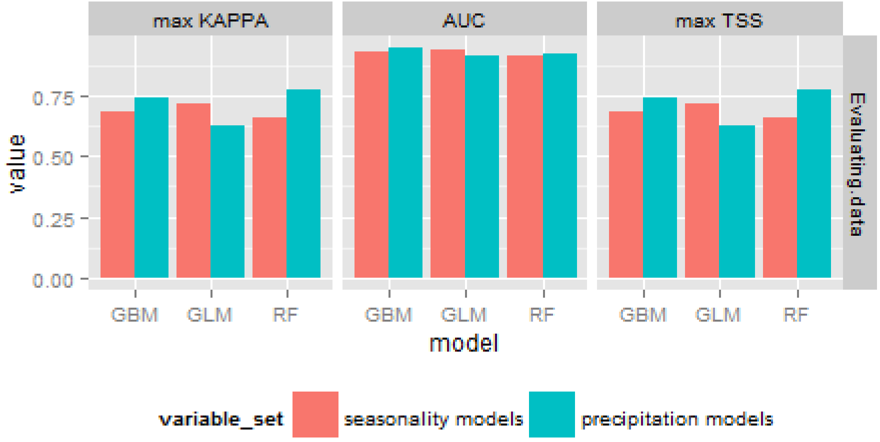
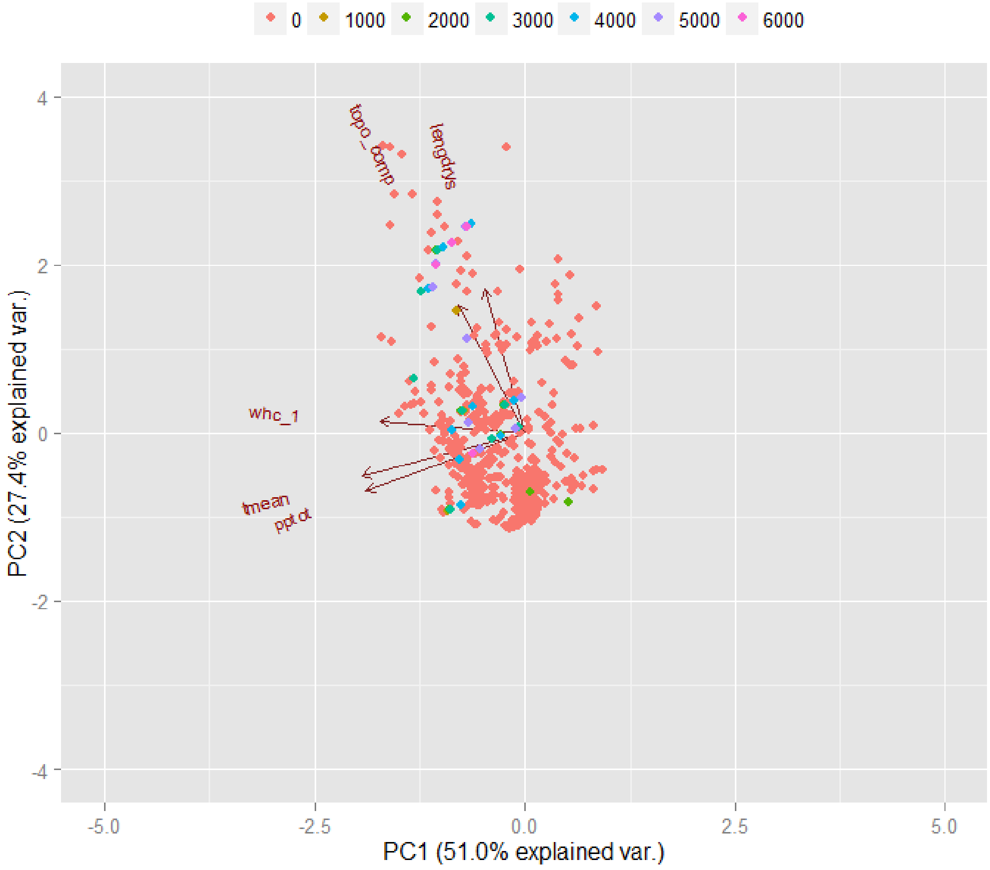


Figure S4 PCA biplot. Environmental conditions for all rainforest presences from all pollen records at each time step and from all pixels with rainforest cover from the African land cover map for 2000 (Mayaux *et al.* 2004)



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CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

Understanding the response of tropical rainforests to past disturbances is of utmost importance to determining and managing the risk that these forests face under current and future drivers of change. This study aimed to improve our current knowledge of the likely future trajectory of the persistence of the tropical Central African rainforest under climate change and fire impact through reconstruction of past vegetation and burning dynamics using palaeoecological records from sedimentary sequences. Four main questions were addressed in this thesis and are further discussed here:

1. What is the role of disturbances driven by fire in determining tropical African forest types? (Chapter 2, Chapter 3 and Chapter 4).
2. Is there a difference in the response of different tropical African forest types to disturbances? (Chapter 3 and Chapter 4).
3. How much change occurred in the distribution of the tropical African rainforest in response to climatic disturbances in the last 6000 years? (Chapter 5).
4. How resilient are African forest types, and the African rainforest as a biome, to past fire and climatic disturbances? (Chapter 2, Chapter 3, Chapter 4, Chapter5).

In this thesis I combined a palaeoecological approach with spatial analyses to understand better the changes in the Central African rainforest. The results are strengthened by the use of several sediment cores from the same region, thus reducing a potential bias caused by one site’s local characteristics. In Table 1 I relate the main questions with the chapters, showing the different hypothesis, data, and main methods for each chapter. Following on from this I discuss the main findings of this thesis.

Table 1 Summary chapters (hypothesis, collected data and analyses) and their relation with the main questions addressed by this thesis (see main text).

Chapter	Question addressed	Subject	Study area	Hypotheses	Collected data	Main analyses
Chapter 2	1, 4	Influence of fires on African forest types.	Sangha River region	1) Either the intensity or occurrence of fires, or both, are different between current forest types. 2) Small and asynchronous fires may be an indication of human-made fires.	Fossil macroscopic charcoal of 12 sediment records spanning 2500 cal BP collected in Swamp, mixed, Marantaceae and monodominant *Gilbertiodendron* forest.	Spatial autocorrelation of fire occurrences. Generalized additive mixed models for fire intensity. Binomial generalized linear models for frequency of fires.
Chapter 3	1, 2, 4	History of Marantaceae forest.	Sangha River region	Marantaceae forest is a result of forest-fire interaction in the Sangha River region rather than a succession from savannah to forest.	Phytoliths and fossil macroscopic charcoal extracted from two sediment records spanning 1200 cal BP collected in current Marantaceae forest.	Temporal cluster analysis. Games-Howell test to test differences in fire frequency. Spearman correlation between vegetation and fire.
Chapter 4	1, 2, 4	History of monodominant *Gilbertiodendron* forest.	Sangha River region	Long term minimal disturbance is a requirement for the presence of the monodominant *Gilbertiodendron* forest.	Fossil pollen and fossil macroscopic charcoal extracted from a sediment record spanning 2700 cal BP collected in monodominant *Gilbertiodendron* forest and published pollen data from other records within the region.	Temporal cluster analysis. Ordination analysis: PCA, CCA.
Chapter 5	3, 4	Changes in rainforest distribution under past climate change.	Central and West Africa rainforest	The African rainforest climatic niche has been stable for the last 6000 years (niche conservatism).	21 fossil pollen records from literature and the African pollen database and paleoclimate layers at 1000 yr step for the last 6000 cal BP.	Biomization method to identify most likely biome for each pollen record through time. Ecological niche models using 3 different algorithms and 2 sets of variables. Model performance analysis using fossil pollen records to validate simulations.

MAIN FINDINGS

1. Role of fire in determining African forest types: A high frequency of fires is required to maintain the Marantaceae forest type.

My results using 12 sediment records demonstrate that local fires were absent in the study area between 2500-1100 cal BP and that the highest peaks of charcoal values occurred in the last 300 cal BP (Chapter 2). After 1100 cal BP fires were spatially discontinuous and asynchronous (no spatial autocorrelation and no correlation between time series of each site) and most sediment records exhibit low values of charcoal influx (average of 0.02 particles/cm^2/yr) throughout. Only one site currently covered by Marantaceae forest shows large values (up to 3.1 particles/cm^2/yr) during the last 200 years.

The apparent individual and localized nature of mostly small fire events suggests that these most probably represent slash and burning activities (Bennett *et al.* 1990) occurring in the Sangha River region over the past 1100 years. Several lines of evidence indicate that humans may have been responsible in particular for the ignition of the majority of fire events after 1100 cal BP: 1) There is no general agreement between different palaeorecords records from Central Africa that a dry event occurred at that time, which may have triggered the fire events (Elenga *et al.* 1994; Reynaud-Farrera *et al.* 1996; Ngomanda *et al.* 2007; Hubau *et al.* 2013), 2) Pottery findings 15 km from the study area are dated between 2000-600 cal BP confirming human presence in the area (Brncic 2002), 3) Bantu migration southwards from Nigeria and Cameroon show two peaks in population density based on increased pottery and metallurgy evidence, of which the second one is believed to have occurred at around 1000 cal BP (Wotzka 2006; Oslisly *et al.* 2013), 4) No major change in species composition is observed in fossil pollen from the two out of 12 records analysed for this chapter at around 1100 cal BP (Brncic *et al.* 2007, 2009).

In addition to determining the cause of ignition of past fires in the study area, I found a difference in fire regimes between forest types. In particular, areas currently covered by Marantaceae forest experienced statistically significantly more frequent fire events in the past than any other forest type (Tovar *et al.* 2014, Chapter 2). Marantaceae forest is typical of the Central African rainforest with a very open canopy and the presence of giant herbs in the understorey, mainly from the Marantaceae family. Previous studies found charcoal layers underneath the soil of this forest type (Brncic 2002) and past burning was observed in current Marantaceae forest (Swaine 1992). My results in Chapter 2 suggest that frequent human burnings played an important role in shaping the current Marantaceae forest. Thus the hypothesis of differences in fire regimes between forest types was confirmed but only for fire frequency while fire intensity was not statistically different between the different forest types.

After obtaining evidence that a high frequency of fire is linked to current presence of Marantaceae forest, it was necessary to analyse the past vegetation changes these sites experienced. Therefore I extracted phytoliths from two of the 12 sediment sequences used in Chapter 2 that are currently covered by Marantaceae forest to describe their vegetation history (Chapter 3). The sequences span 750 and 1250 cal BP and for both sites there is a change from mixed forest to Marantaceae forest at around resp. 450 and 600 cal BP. Although previous hypothesis suggested that Marantaceae forest may be a succession from savannah to forest (Letouzey 1968; de Foresta 1990; White 2001b), my results show the opposite: a transition from a mature forest (mixed forest) to a more open canopy forest (Marantaceae forest) in the Sangha River region.

For the Sangha River region I suggest that the maintenance of Marantaceae forest until present time is related to fire because there is a statistically significantly higher charcoal frequency during the period when Marantaceae forest dominated than when mixed forest dominated. Furthermore I suggest that Marantaceae forest represents an alternative stable state to mixed forest. Results show that the presence of Marantaceae forest is more closely related to the opening of the canopy (a significant negative correlation between phytoliths of broad-leaved trees and frequency of fires) (Chapter 3). Therefore, the mechanism I proposed is a combination of three steps. First, basal sprouting post fire, which is typical of rainforest (Marrinan *et al.* 2005; Knox & Clarke 2012), is suppressed by subsequent fires (Ainsworth & Kauffman 2013).This leads to an increase in canopy opening. Second, previously established Marantaceae herbs or new individuals of Marantaceae species spread due to the opening of the canopy. Third, the Marantaceae herbs grow and cause extensive soil light reduction due to their large leaves and higher below ground competition because of the development of a dense rhizome system thus supressing any other tree regeneration (Brncic 2002; Gillet 2013). In addition to light reduction and below ground competition, the presence of these giant herbs and the open canopy would have made the spreading of fires easier. Humans may have used the leaves as fuel and the open canopy allows a better mixing of the moist air masses below the forest canopy with the dryer and hotter air above (Ray, Neptstad & Moutinho 2005). In this way a positive feedback establishes between Marantaceae forest and fires leading to the existence of alternative stable states.

Few studies exist that have used continuous charcoal records, and this thesis is the first to use a collection of cores to arrive to conclusions about the relationship between forest and fires. Much has been done in terms of how fires affect forest and savannah not only for Africa but for the Neotropics, proposing different models (Lehmann *et al.* 2011; Murphy & Bowman 2012). Here for the first time we address the influence of fires in forest types. The usefulness of these results has been highlighted already (McGuire & Davis 2014) as an important contribution to a future improvement of distribution models, because my results show the importance of including fires and human disturbances in these models.

2. Differences in responses to disturbances between forest types: Forest types have responded differently to past fires and past climate change

Results from different chapters of this thesis (Chapter 2, 3 and 4) show that the mixed forest type is the forest type most affected by both fire and climatic disturbances. Although areas currently covered by mixed forest have experienced different levels of small past fires (Chapter 2) more frequent fires can cause a major change in vegetation composition (Chapter 3). I show that two sediment records evidence a change from mixed forest to Marantaceae forest and that Marantaceae forest maintenance is related to a high frequency of fires (Chapter 3 and see previous section). Drivers triggering the change from mixed forest to Marantaceae forest in the Sangha

River region may involve other factors than only fire, however, once the change is made and the feedback with fires is established the observed pattern of Marantaceae forest permanence is highly likely (Chapter 3). Therefore, an increase of human fires in the region may lead to a higher presence of Marantaceae forest, in its turn leading to a decrease in important species from the mixed forest.

The effect of climate change on mixed forest is also apparent from the analysis carried out in Chapter 5. For this chapter I gathered all pollen records from Tropical Central and West Africa that were available in the literature and used these to calculate the most likely biome based on pollen composition for the last 6000 cal BP. The different authors that published the vegetation records already described the changes for each pollen record individually, but applying the biomization method to all records allowed me to make a better comparison between sites to analyse whether changes in biome occurred for each site. Twelve of the 21 pollen records used in Chapter 5 represent mixed forest before the dry climatic event that occurred at around 3000-2500 cal BP (Goualougo, Nyabessan, Lake Nguene, Mopo Bai, Lake Barombi, Lake Mbalang, Lake Bosumtwi, Lake Ossa, Ngamakala pond, Lake Sinnda, Lake Sele and Bilanko, see references in Chapter 5). The most dramatic forest response to the climatic event is a change from mixed forest to savannah observed at Lake Sele, Lake Mbalang and Lake Sinnda, while Ngamakala pond showed an increase of savannah in the surroundings with interspersed rainforest patches. The records that exhibited the most dramatic change are located currently close to the rainforest borders. The other records did not show a change to savannah but instead an increase of deciduous species (i.e. a higher affinity with the seasonal forest biome). All but one site (Lake Bosumtwi) demonstrated changes in their vegetation composition, indicating the vulnerability of the mixed forest type to climate change.

In the case of the Marantaceae forest type, the previous section showed that it has been highly favoured by fire disturbances and it appears to require a high frequencies of fires to be maintained (Chapter 2 and Chapter 3). However the question remains whether we can find Marantaceae forest before 600 cal BP in other regions than in the Sangha River region. The apparent recent appearance of Marantaceae forest in our study area prevents the analysis of how this forest type will cope under climate change.

Lastly, for the monodominant *Gilbertiodendron* forest, my analysis of past vegetation for the last 2700 cal BP of a currently monodominant patch using fossil pollen detects no response of this forest type to climate change (Chapter 4). Although climate change was not measured directly in this study, dry events for the last 2700 cal BP have been shown to have occurred throughout this region from several other studies examining palaeoclimatic change as indicated in fossil proxies including isotopes, diatoms, fossil pollen, and geochemical analysis (e.g. Nguetsop *et al.* 2004; Schefuß *et al.* 2005; Brncic *et al.* 2009; Ngomanda *et al.* 2009b). The detection of periods with different vegetation composition (zonation) using both an optimal partitioning approach and agglomerative technique detect only 1 meaningful period, implying that the composition mostly remained unchanged for the last 2700 cal BP. Moreover, *Gilbertiodendron* fossil pollen was always present and its relative abundance remained more or less constant over time. From this I conclude that the monodominant *Gilbertiodendron* forest appears to be more resilient to climate changes that occurred, during this interval in time, than other forest types.

In relation to fires, monodominant *Gilbertiodendron* forest also seems to be unaffected by recent (300 years) and small fires again as evidenced by little change in its composition. However these results should be treated with caution because it is possible that the charcoal contribution may have come from the borders of the small lake rather than from the monodominant stand itself. Nevertheless, results from this study certainly appear to be in support of the hypothesis that long-term absence of fires are required for the maintenance of the monodominant forest and that the forests have an unexpected high resilience to climate change in comparison to mixed forest.

3. Changes in forest distribution under past climate change: the rainforest climatic niche has not been stable during the last 6000 years

In Chapter 5, ecological niche models were used to model current rainforest distribution and simulate distributions at 1000 year time steps for the last 6000 cal BP and were tested against fossil pollen records. I used two sets of ecological niche models, i.e. one set using precipitation and other using length of dry season as proxy for water availability. Both set of models performed well at present time when compared to points extracted from current land cover maps. For the past period (last 6000 cal BP) the models were compared to the pollen records, and here they showed diverging behaviour. The models using the length of dry season matched the pollen records noticeably worse than the models using precipitation as explanatory variable between 6000 and 4000 cal BP. However, the match between models using the length of dry season with pollen records improved considerably after 4000 cal BP. From this I concluded that relative importance of drivers of rainforest distribution may have changed over time. One potential explanation is that precipitation may have overridden the effect of the length of dry season for the period between 6000 and 4000 cal BP because total annual precipitation was higher than at present time. Also, the length of the dry season may have become more important only in the last 3000 cal BP due to the lower precipitation levels. Under a lower precipitation scenario, water availability is more restricted and therefore the resistance of rainforest to a longer dry season becomes more difficult.

Regardless of cause, these results provide evidence that the climatic niche of the African rainforest has not been stable over time and has partially shifted. This implies that longer dry seasons may have existed in the past, even though the levels of precipitation driving rainforest distribution may have been stable. This is a controversial finding because to date, climatic niche stability is generally assumed.

The past distribution of African rainforest was previously inferred from individual pollen records and no regional assessment of the extent of these forests was attempted to date. Chapter 5 is therefore the first study to simulate past distribution using ecological niche models. The best two models use precipitation as a proxy for water availability. Simulations of both models locate the northern border of the rainforest between 8°N and 10°N at 6000 cal BP, which implies that its extension was between 9-17 % larger than the simulated present distribution. The models agree less on the levels of rainforest fragmentation for the last 6000 cal BP. One model shows an intact forest block in Central Africa (extending from East Ghana to Democratic Republic of Congo). The other model simulates a rainforest that was always fragmented in the centre part. Fragmentation intensified around 3000 cal BP, which is when the dry event occurred. However, the fragmentation simulated by the model is not as strong as suggested by some authors (e.g. Maley 2002). Further analysis will be necessary to corroborate the two potential patterns that have emerged from the models implemented in Chapter 5.

The integration of pollen records using a spatial model allowed me to integrate a much larger number of pollen records than traditional palaeoecological studies, which typically rely on data from a single core. Nevertheless, this number is still very low to be representative of the size of the study region, and is a major limitation for corroborating hypotheses such as the level of fragmentation caused by dry events.

4. African rainforest resilience: Putting all the pieces together

In this thesis I refer to resilience as the capacity of the rainforest/forest type to absorb disturbances and re-organize in the face of the change as a way to retain a similar structure and functioning (Scheffer 2009). Table 2 summarizes the current knowledge about African rainforest resilience, as well as the contributions of this thesis. African rainforest resilience has been mostly studied at the biome level where the measured variable is typically either the forest cover or the biomass. This is not a surprise considering that the African rainforests is the second largest block of forest of the world (Primack & Corlett 2005) and therefore is a large contributor to global carbon stocks (Justice *et al.* 2001; Lewis *et al.* 2013). What we currently know is that, in the short-term the tree cover/biomass of the African rainforest appear to be resilient to moderate climate change (Fauset *et al.* 2012; Asefi-Najafabady & Saatchi 2013) and that in the longer term (decades to millennia) it shows faster rates of recovery than other rainforests after disturbances (Cole *et al.* 2014). This resilience is also shown in future projections of rainforest range and carbon stock (Zelazowski *et al.* 2011; Huntingford *et al.* 2013).

Table 2 Resilience of African rainforest at biome and forest type level to climate change disturbances (warmer and drier) and to fires. In black the contribution of the present thesis. In grey are results from previous studies.

Resilience to disturbance		FOREST TYPE LEVEL			BIOME LEVEL
		Marantaceae forest	Mixed forest	Monodominant forest	Lowland rainforest
LONG TERM (>CENTURIES)	Resilience to fires	**High** Frequent fires are required for its maintenance	**Low** High frequency can lead to a change into Marantaceae forest	**?** Fires were mainly absent in collected records	-
	Resilience to climate change	-	**Low** Most mixed forest records had experienced change in vegetation composition	**High** No change in species composition is observed in response to dry events	**Low/High?** Change of climatic niche. **High** High rate of forest recovery after disturbances (Cole et al. 2014)
SHOSRT TERM (DECADES)	Resilience to fires	-	-	-	-
	Resilience to climate change	-	**High** For biomass (Fauset et al. 2012) Low For species composition (Fauset et al. 2012)	-	High Canopy structure (Asefi-Najafabady & Saatchi 2013)

- indicates that this has not been analysed
? indicates that it was not possible to determine a clear pattern from the data available

This thesis contributes to an increased understanding of resilience of ecological processes at a long-term (> centuries) time scale and at the level of a finer analysis unit than the biome, i.e., the forest types. This allows incorporation of species composition as defined by forest type, instead of only the characteristic of tree cover and biomass as has been explored previously. The results of this analysis shed light on the different responses of forest types to climate and fire disturbances. In particular, monodominant *Gilbertiodendron* forest seems to be the most resilient forest type of those studied in this thesis to small climate change events (drier periods) with no significant change in species composition. Questions remain about the mechanisms behind this apparent resilience and efforts should be geared towards their better understanding including looking at the traits of *Gilbertiodendron*. However from the ecology of this forest we know that its reproduction depends on large seeds that are difficult to disperse and shade conditions. Therefore, looking to the future any major opening of the canopy may seriously affect its continuity and human activities such as logging or any other activity that implies opening of the canopy, may represent a major threat for this forest type.

In comparison, work from this thesis indicates that Marantaceae forest is resilient to fires but it is unknown how it would respond to climate change. Lastly, mixed forest remains as the less resilient forest type to both, climate change and fires.

At the biome level, models developed in Chapter 5 suggest that the African rainforest underwent no major rainforest fragmentation during or after the dry period of around 3000 cal BP. Although this needs to be corroborated with more pollen records, the broad maintenance of the forest tree cover has also been suggested by other studies (Malhi *et al.* 2013). The models also show that rainforest in the core area may have been able to cope better with climate change than rainforest adjacent to other biomes. This is based on the evidence from the record collected in *Gilbertiodendron* forest which shows no significant change in species composition. However, further work is needed at the species diversity level in addition to the biome level and forest types, especially when it has been shown that species composition is affected by drier conditions in the short term (Fauset *et al.* 2012) and that large-scale disturbance reduces diversity as well (van Gemerden *et al.* 2003).

The second important finding at the biome level is that its climatic niche does not appear to show stability over the last 6000 cal BP. Although the range of total annual precipitation required for rainforest presence remains the same over time, the length of the dry season becomes important in defining rainforest distribution only in the last 3000 cal BP. This finding has important consequences for future projections under climate change scenarios and the use of total annual precipitation should be preferred over the length of the dry season.

In section 1 of main findings I show that most of the fires occurring in the Sangha River region in the past 1100 cal BP, are probably caused by human ignitions (Chapter 2). I also showed that frequent past burning have led to changes in vegetation composition from one forest type to another one (Chapter 3). Despite the observed changes in composition as a result of the human intervention, the area remained forested. However, a potential future disturbance, such as an increase in fire activities associated with agriculture may put the rainforest at a higher risk than it has faced during past fire disturbances.

It has been highlighted previously that the higher resilience of tropical African rainforests over the other tropical rainforests may be related to its history of disturbances (Malhi *et al.* 2013). Here I show that both a single forest type (monodominant *Gilbertiodendron* forest) as well as the biome as a whole are indeed somehow resilient to climate change events but not necessarily to fire disturbances. Future projected disturbances are likely to be higher than those that occurred in the past. For example, future climate change is projected to occur at a faster rate than in the past 6000 years (Taylor, Stouffer & Meehl 2012) and the increase of human activities using slash and burning has being observed more frequently (Cochrane 2003). Therefore, we should be aware of the limits of pressure that can be exerted on the forest. This thesis contributes to the body of evidence that helps understanding how rainforests have responded to disturbances.

FUTURE RESEARCH DIRECTIONS

The analyses presented in this thesis have contributed to African rainforest responses to disturbances, yet it has also opened new questions related to our understanding of the disturbances themselves, as well as the impact of these disturbances on the vegetation. Below I list the most important topics and knowledge gaps to be addressed for future research:

1) Further analysis of charcoal from sediment records across the region is necessary to understand better the dynamics of fires. Another interesting approach that fossil charcoal allows is the identification of species that were burned by using anthracology. This approach has provided useful information in areas such as the Ituri forest in Democratic Republic of Congo (Hart *et al.* 1996) and in the Mayumbe region in the Republic of Congo (Hubau *et al.* 2013). Such an approach is suitable for the Sangha River region and will help to complement the findings of this thesis.

2) Our knowledge of the current African climate remains limited and the reconstruction of past climate is even more challenging. A good opportunity to generate better data on the past climate would be the use of hydrogen isotopes from leaf waxes within the core of the African rainforest. This relatively new technique has already shown good results for example in Lake Challa in East Africa (Tierney *et al.* 2011). Therefore it has good potential to be applied in my study area.

3) This thesis opens new questions about the responses of African forest types with climate. For example: What would be the impact of climate change in Marantaceae forest? Or what is the threshold of climatic impact that *Gilbertiodendron* forest can manage? For this last question the analysis of patches of different size, and analyses spanning a longer time period than 3000 cal BP would increase our knowledge about monodominant forest.

4) In terms of resilience, the identification of thresholds at which rainforest cross from one state to another (e.g. from one biome to another or from one forest type to another) should be a priority. This requires the study of the disturbances and the response separately, in order to integrate them independently in a model framework. As mentioned before, high resolution climatic data from sediment sequences will allow a better understanding of past fluctuations in climate. In the same way high resolution analysis of pollen records will allow a better understanding of the vegetation responses.

5) Geographically, the Democratic Republic of Congo remains the most understudied country in terms of pollen records. The exploration of this region will give invaluable insights of the core area of the rainforest allowing us to complement our current knowledge of rainforest responses to past disturbances.

All these questions and knowledge gaps show that there is still much work to be done to understand better the African rainforests ecology and resilience. This thesis represents the first step towards filling these gaps and providing more information of the past responses of this globally important forest block.

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APPENDIX 1: DECLARATION OF AUTHORSHIP

UNIVERSITY OF
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19 June 2015

Examination School

University of Oxford

To whom it may correspond

I declare that the manuscripts presented as Chapters 2 to inclusive within this thesis, for which I am co-author, are substantially the work of Mrs Carolina Tovar Ingar, the author of this thesis, and that my role has been limited to supervisory input and comments on drafts.

Yours sincerely,

Professor Kathy J. Willis

Department of Zoology

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Kew
ROYAL BOTANIC GARDENS

13 June 2015

Examination School
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Dear Sir/Madam,

Papers submitted by Carolina Tovar Ingar

I declare that the manuscripts presented as Chapters 2 to 5 inclusive within this thesis, for which I am co-author, are substantially the work of Mrs Carolina Tovar Ingar, the author of this thesis, and that my role has been limited to supervisory input and comments on drafts.

Yours sincerely,

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Co-supervisor

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APPENDIX 2: REVIEW PAPER

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Review

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Determining the response of African biota to climate change: using the past to model the future

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Prediction of biotic responses to future climate change in tropical Africa tends to be based on two modelling approaches: bioclimatic species envelope models and dynamic vegetation models. Another complementary but underused approach is to examine biotic responses to similar climatic changes in the past as evidenced in fossil and historical records. This paper reviews these records and highlights the information that they provide in terms of understanding the local- and regional-scale responses of African vegetation to future climate change. A key point that emerges is that a move to warmer and wetter conditions in the past resulted in a large increase in biomass and a range distribution of woody plants up to 400–500 km north of its present location, the so-called greening of the Sahara. By contrast, a transition to warmer and drier conditions resulted in a reduction in woody vegetation in many regions and an increase in grass/savanna-dominated landscapes. The rapid rate of climate warming coming into the current interglacial resulted in a dramatic increase in community turnover, but there is little evidence for widespread extinctions. However, huge variation in biotic response in both space and time is apparent with, in some cases, totally different responses to the same climatic driver. This highlights the importance of local features such as soils, topography and also internal biotic factors in determining responses and resilience of the African biota to climate change, information that is difficult to obtain from modelling but is abundant in palaeoecological records.

1. Introduction

Tropical and subtropical African biomes, in particular forests and savannas, have long been recognized for their important ecosystem services and associated human benefits. African forests are valued for both their importance in terms of regulating (e.g. CO_2 drawdown [1]) and provisioning services (e.g. timber, non-timber forest products [2]) and savannas for their potential in terms of provisioning and cultural services, for example, grazing land for both animal husbandry and ecotourism [3]. Most recently, these African landscapes have also been highlighted in terms of their provisioning services for biofuels [4]. Determination of these current ecosystem services at regional and landscape scales and the valuation of these benefits is the focus of much research presently (see examples in the electronic supplementary material, table S1). However, it is also recognized that these ecosystem services are changing in response to changes in climate and this will have a significant impact on provision of services in the future [5]. A key research challenge is to quantify the impact of these forecasted climatic changes on the African tropical and subtropical biota which are important for current and future ecosystem service provision.

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There are currently two main approaches to assess the impact of future climate change on African biota: (i) modelling the response of species and/or vegetation functional units to changes in climate, i.e. using the present distribution of biota/climate to develop models to predict future change; and (ii) analysing the palaeo-record, i.e. to examine past biotic responses to climate changes analogous to forecasted climate to determine rates and possible direction of future responses to climate change.

Modelling approaches to assess the impact of future climate change on biota include bioclimatic envelope models and dynamic vegetation models. In the first, present-day distribution of the species in relation to the climatic envelope is calculated, and this climate/distributional range is then used to predict future range shifts in response to climate change (for a review, see [6]). In Africa, a number of studies have been carried out using this approach, indicating that for some species, significant loss of suitable climate space will result in extinctions. For example, a modelling study of 227 African mammals using climate predictions for 2050 and 2080 from the HadCM3 general circulation model (Intergovernmental Panel on Climate Change (IPCC) special report on emissions scenarios A2 and B2 [7]) indicated that between 25 and 40% of the species modelled will be critically endangered or extinct by 2080 [8]. Similarly, modelled range shifts for 5197 sub-Saharan plant species, using the same general circulation model, predicted the extinction of between 25 and 42% of species by 2085 due to reduction in suitable climate space, especially in the Guineo-Congolian forest [9]. It is widely acknowledged, however, that these models are highly sensitive to the algorithms used [10,11]. Moreover, they are unable to robustly quantify vegetation responses to conditions outside the range of variability of their training datasets (i.e. non-analogous [12–14]), such as future high CO_2 atmospheric concentration or temperatures not observed currently. Differences in the assumptions made regarding non-analogous conditions might result in virtually opposite forecasts of extinction risks [15]. Other problems include an often poor understanding of the full ecological tolerances of the modelled plants/animals, determination of the full spectrum of biotic interactions, and coarse spatial scales (approx. 100 km grid squares) [6].

Dynamic vegetation models surmount many of the above-mentioned limitations, as they are mechanistic and explicitly formulate physiological, biophysical and biogeochemical processes as well as species interactions [16], and can thus be used to predict ecosystem response in non-analogous scenarios [17–19]. In particular, coupled vegetation dynamics and climate models have been used to demonstrate the importance of vegetation and land-cover feedbacks in the strength of the African monsoon over West Africa [20–22]. Despite their great insights and usefulness, the complexity of dynamic vegetation models means that they are very often used with plant functional types (PFTs) instead of species (e.g. tropical broad-leaved evergreen, temperate needle-leaved evergreen, etc.) [19,23] and at coarse resolution: as a result, the use of PFTs does not enable these models to account for the observed individual species responses to environmental changes [24].

The use of historical and palaeo-records to determine possible biotic responses to future climate change has been less used to date. This is, in part, due to perceived circularities stemming from the use of proxies such as fossil pollen as both climatic and biological sources of information. The introduction of new tools and proxies in recent years has, however, resulted in a growing body of palaeoclimate-proxy evidence that is independent of the fossil data detailing biotic response (table 1). This paper presents a review of some of these newly emerging datasets alongside the fossil evidence for biotic responses to examine the insights that these palaeo-records can provide on the potential responses of African biota to projected future changes in climate. It focuses on three regional forecast climate scenarios in Africa, namely enhanced wetness, enhanced aridity and faster rates of climate warming. Fossil evidence for spatial variations in biota in response to climate change in Sahara, West Africa, East Africa and Southern Africa is examined and then discussed in the context of the information that they provide for determining current and future changes of biota to predicted climate changes.

2. Current and future climate change in tropical and subtropical Africa

In order to simplify the great diversity of climates across Africa, we have used the regional division used by the IPCC [25] to narrow the focus of our review, namely to consider records from Sahara, West Africa, East Africa and Southern Africa (see the electronic supplementary material, figure S1). Near the equator, within the inter-tropical convergence zone (ITCZ), high precipitation (with equinoctial maxima) is mostly modulated by insolation, and regional variability is due to the influence of orography and oceans. North and south of this region, climate is dominated by the African monsoon system ([26]; see the electronic supplementary material, figure S1). Subtropical West Africa experiences one rainy season (May to September), modulated to a great extent by El Niño–Southern Oscillation (ENSO), sea surface temperatures (SSTs) over the Atlantic, and strong land–atmosphere interactions [27,28]. Subtropical East Africa in comparison experiences two rainy seasons, the ‘long rains’ (March to May) and the highly variable ‘short rains’ (September to December) [29,30], driven by the seasonal migration of the ITCZ and the movement of the Congo Air Boundary (figure 1) [34]. Finally, Southern African climate is highly variable regionally and modulated by the Atlantic and Indian oceans [35–38] as well as ENSO [39,40].

Given the diversity of the current climate in Africa, it is not surprising that climate predictions for this continent are also highly complex. From the most recent IPCC records, the following can be summarized for changes to the African climate by the end of this century (2080–2099):

- precipitation forecasts indicate high regional variability within Africa; some regions will get drier and other regions wetter. In East Africa, precipitation will probably increase during the ‘short rains’ season (October to December; [30,41]). In comparison, Southern Africa’s climate is robustly predicted to get drier [42], especially in the austral winter [43] and to a lesser degree in spring and summer [44]. The Sahara is expected to stay dry or become drier [45]. Finally, in the Sahel and West Africa it could get wetter or drier [21,46–48], because despite recent improvements in the coupled model inter-comparison project phase 5 [49], there is still substantial inter-model spread in model projections (especially in the duration and intensity of the rainy season in the Sahel [27,50,51]);
- rate of climate change will increase. James *et al.* [52] report high inter-model agreement (from a total of 24

Table 1. Temperature and wetness phases in Africa over the past 25 000 cal year BP, based on palaeo-proxies. Information of location and references for each record and the proxies used is detailed in figure 1 and the electronic supplementary material, table S2 following the number attached to each site name. Where absolute values are provided in the source publications, these are given in the electronic supplementary material, table S3. All other proxy interpretations are taken directly from the original source data. 'isotopes': isotopic and molecular climate proxy data; 'mixed': pollen (biotic response) included.

region	Sahara		West Africa									
proxy	isotopes	mixed	isotopes			pollen						
name / age	1. GeoB9508	2. Yoa	3. GeoB4905	4. GeoB6518	5. ODP1078c	6. ODP1078	7. Ossa	8. Kitina	9. Barombi Mbo	10. Ngamakala	11. Mbalang	12. Bosumtwi
500		warm and very dry	warm and dry	warm and dry	warm and dry	warm and dry	warm and wet	warm and wet	warm and wet		warm and dry	warm and wet
1000	dry							warm and dry		warm and wet		
2000							warm and dry		warm and dry	warm and dry		
3000		warm and dry	warm	warm and wet	warm		warm and wet	warm and wet	warm and wet		warm and wet	
4000	wet	warm and wet				warm and wet				warm and wet		
5000												
6000			warm and wet		warm and wet						cold and wet	
7000	dry											
8000			warm		warm	warm and dry						
9000	wet											cold and dry
10 000						warm and wet						
11 000	dry			warm and dry								
12 000					transition warm/cold				warm and dry			
13 000	wet			cold and dry					warm and wet			
14 000												
15 000	dry		cold		cold	cold			cold and dry			
16 000			cold and dry		cold and dry					cold and dry		
17 000												
18 000												
19 000						warm and wet						
20 000												
21 000												

region	East Africa									Southern Africa	
proxy	isotopes				pollen				mixed	isotopes	
name/age	13. Lake Challa	14. Tanganyika	15. Lake Victoria	16. Malawi	17. Lake Albert	18. Masoko	19. Lake Naivasha	20. Tanganyika	21. Lake Victoria	22. Namibia	23. GeoB9307
500	dry	warm and dry			warm and dry	wet	warm and very dry	warm and dry	warm and very dry	dry	cold and wet
1000			warm and dry	warm and wet							
2000			cold and dry								
3000				warm and dry				warm and wet	warm and dry		cold and dry
4000					?	warm and dry				dry/wet	
5000	wet	warm and wet					warm and dry				
6000			warm and wet						seasonally wet		warm and dry
7000				cold and wet							
8000							warm and wet		warm and wet	wet conditions	
9000				warm and dry							
10 000					warm and wet						
11 000			cold and dry	warm and wet				cold and dry			warm and wet
12 000	dry	warm and dry			abrupt aridity	warm and wet			cold and dry		
13 000	wet	cold and dry			warm and wet						warm and dry
14 000					cold and very dry	cold and wet	cold and dry				
15 000	dry										warm and wet
16 000				cold and wet		warm and wet					
17 000							cool and moist				
18 000											
19 000											
20 000	wet										
21 000											

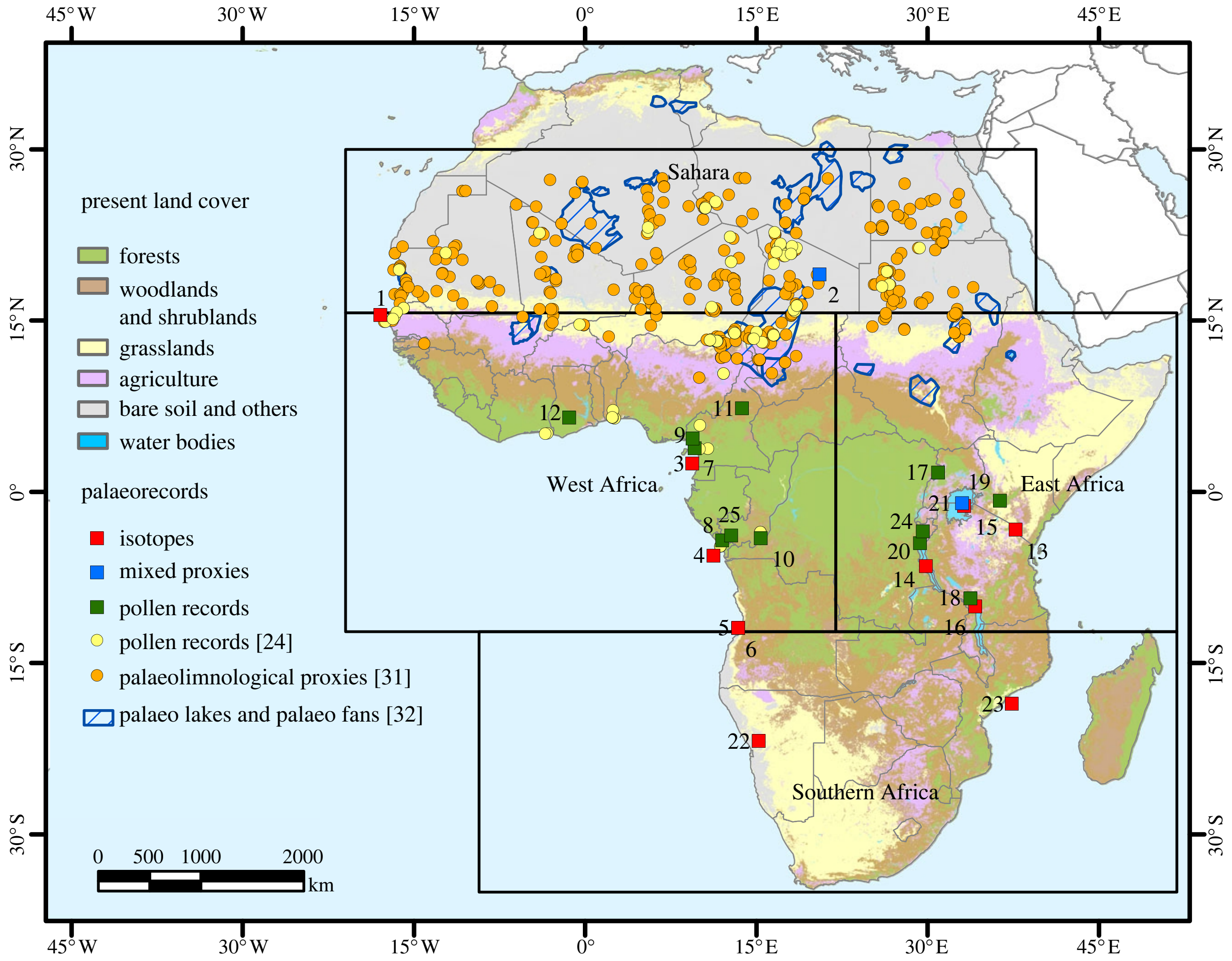

Figure 1. Location of the main palaeo-records in Africa. Squares: palaeo-records explicitly mentioned in the text (numbers as in table 1). Names and description in the electronic supplementary material, table S2. Mixed proxies involved a combination of pollen, molecular proxies and/or diatoms. Circles: records from other palaeo-record compilations mentioned in the text [24,31]. Main water bodies during the African humid period obtained from [32]. Present land cover based on [33]. African regions based on [25].

global climate models, GCMs) in predictions on faster warming rates over Africa than the global average; and

— temperature projections from CIMP5 [53] for the late-twenty-first century indicate warming in all months of the year in all African regions. Scenario-dependent (ranging from RCP2.8 to RCP8.5 [53]) temperature increases range from approximately 1.0°C to 4.4°C and in some cases 5.1°C in all African regions (as defined in [25]) and in both winter and summer months.

3. Biotic responses to past climate conditions analogous to projected scenarios

Fossil proxy climate evidence indicates that many of these predicted climatic changes for the African continent (warmer and wetter; warmer and drier; and increased rates of climate warming) of similar magnitudes have also been encountered in the past. Section 3*a* examines the evidence for these past climatic fluctuations and the biotic responses to them.

(a) Warmer and wetter

There is now considerable independent palaeoclimatological evidence to suggest that warmer and wetter conditions occurred throughout many parts of western Africa, eastern Africa and the Sahara between approximately 11 000–4000 cal year BP, an interval commonly known as the African Humid Period (AHP) [17,31,54–60] (table 1). Current understanding of the causes of these conditions points towards a general response to changes in insolation, which in East Africa was associated with an increase in dry season precipitation (and thus a reduction in seasonality [17]) and in West Africa with an increased penetration of an enhanced west African monsoon [21], with increased overall precipitation.

Mapping and dating of palaeo-river channels, closed basins, palaeo-lake shorelines and spillways demonstrates that the vast Saharan region from approximately 11 000 to 8000 cal year BP contained a series of linked lakes, rivers and inland deltas comprising a large interlinked waterway, channelling water, plants and animals into and across it [31,32] (figure 1). In addition, deuterium/hydrogen isotopes of leaf waxes (proxy for wetness) indicate wetter conditions in Sahara and West Africa (table 1) [61,62], and alkenone-derived SST reconstructions (proxy for temperature) indicate regionally warmer conditions in West Africa [63] (table 1).

Palaeoecological evidence indicates that biotic responses to this interval of enhanced wetness were dramatic. In the Sahara and West Africa, pollen-based vegetation reconstruction from 73 sites (located between 4.3° S and 25.5° N; figure 1) [24] indicates a northward progression of many woody species into areas that are now classified as Saharan desert: a range expansion of up to 400–500 km northward of present range. This resulted in some tropical trees growing at 15°N in an area that is currently occupied by the Sahara desert [24]. Diversity reached a maximum at approximately 8.5 ka when Saharan/Sahelian elements which persisted throughout this period were mixed with savanna and forest species of Guineo-Congolian, Guineo-Sudanian and Sudanian affinities from the more humid south. All species studied indicate an individualistic rate and direction of movement, probably via water courses and gallery forests [24,32,64]. Thus, with this warmer and wetter climate, some regions that are now plantless hyperarid deserts were occupied by savanna, desert grassland [54,65] and in some places gallery forests [24], resulting in complex ‘non-analogue’ vegetation assemblages with mixed xeric–semimesic–mesic vegetation that has no modern counterpart.

In East Africa, palaeoenvironmental records including TEX86 (an organic palaeothermometer), deuterium/hydrogen and carbon isotope ratios of higher plant leaf waxes (proxy measures of palaeo-wetness) from Lake Tanganyika [60] (figure 1 and table 1) indicate that major changes in vegetation were highly correlated to climate trends during the wetter and warmer period 11 500–5000 cal year BP. Overall, the trend towards warmer and wetter conditions was paralleled by a shift in vegetation from one dominated by savanna and C_4 grasses [66,67] to a landscape dominated by C_3 trees and shrubs [66].

Significant, region-wide changes in vegetation therefore occurred in response to enhanced temperature and precipitation. These included large-scale range shifts, development of novel plant assemblages, higher concentrations of plant biomass in regions previously unable to support woody tree growth and extensive community turnover and assemblage change. However, the responses of plants appear to have been individualistic; there is little support, for example, for a vast ‘wave’ of forest migration—rather different species underwent range shift at different rates (varying in their response by thousands of years) and in different directions, and the overall response was nonlinear [24,32,64] and appears to have been strongly influenced by local abiotic factors.

(b) Warmer and drier

Palaeoclimatic evidence indicates that a transition into a significantly drier climate occurred in some parts of Africa during the period 4000–1000 cal year BP (table 1). For example, in West Africa, deuterium/hydrogen isotopes from leaf waxes (proxy for wetness) and alkenone-derived SST reconstructions (proxy for temperature) indicate a decrease in wetness from 3200 cal year BP onwards and increase in temperature [63] (table 1).

In equatorial West Africa, one of the best records depicting biotic response to enhanced aridity is found in the fossil pollen sequence from Lake Mbalang, central Cameroon at approximately 7°N (figure 1) [68]. Around this site, palaeoecological evidence indicates there was a large-scale reduction in tropical forest, and the modern savanna became established around 3000 cal year BP (figure 1 and table 1). Lakes such as Sinnda completely dried up between 4000 and 1200 cal year BP [69]. Here, the structure of the forest changed significantly to favour dry-adapted semi-deciduous taxa, and disappeared altogether (4000–1200 cal year BP [69]) to the current grasslands. This forest response however was not uniform, with evidence from palaeoecogical records obtained from lakes Ngakamala, Kitina and Barombi Mbo (figure 1) indicating only the fragmentation of the forest and the appearance of savanna mosaics during the same interval of aridity [70–72]. Around Lake Ossa [73], there was a change in forest composition with an increase in pioneer species (*Alchornea* and *Macaranga*), whereas at Bosumtwi, almost no response is seen in the palaeo-record of vegetation [74]. This apparently local response of vegetation across West Africa to the same climatic forcing testifies to the importance of localized edaphic and geomorphic contexts and the variability in the stability and resilience of local vegetation structure to regional-scale climatic perturbations.

In East Africa, abrupt changes towards arid conditions are also recorded in the Tanganyika basin during the mid-Holocene, where an independent precipitation proxy (deuterium/hydrogen isotopes from plant waxes) indicates moderate drying from 6200 to 5500 cal year BP and a subsequent abrupt shift to arid conditions at 4900–4500 cal year BP [60]. Despite these rapid threshold-like shifts in hydrology, the vegetation record exhibited a gradual evolution towards C_4 dominated grasslands from 11 000 cal year BP and then throughout the Holocene. At this site, xeric grassland/shrubland therefore showed an apparent strong internal ecosystem control, being to some extent resilient to observed climatic swings [60]. From around 2700 cal year BP to present, however, a reduction of arboreal species and expansion of the current grasses occurred [75].

Direction and timing of past vegetation change in response to warmer and drier climate in Africa was therefore often nonlinear, highly variable spatially and appears to have been dependent on specific ecosystem resilience to aridity at the local and regional scale. Assemblage change occurred in some areas, but there is little evidence to indicate a uniform change from forest to savanna or grassland; rather local factors seemed to strongly influence both the type and also timing of the response with some vegetation assemblages/areas displaying far greater resilience to enhanced aridity than others.

(c) Faster rates of warming

IPCC GCMs indicate that Africa will undergo a net warming of 3–4°C by 2100, with mean predicted rates of warming more than 0.3°C per decade. These rates are a conservative number, because they are higher regionally (subtropics), under larger emissions scenarios and vary seasonally (i.e. June to July) [52,53]. A useful interval in time to examine past biotic responses to similarly rapid warming rates is during the transition coming into the present interglacial (for a review, see [76]). Palaeoclimatic estimates indicate that the rates encountered at this interval are roughly comparable with estimates of warming over the twenty-first century [76,77]. For example, at the higher latitudes of the Northern Hemisphere, the rapid warming at approximately 11.7 to 11.5 ka produced increases of 5°C and more over a few decades [78], and data from Greenland ice cores suggest that a more than 10°C warming may have occurred in a period of 20–60 years [79]. Evidence from Lake Masoko, East Africa (see the electronic supplementary material, figure S2), indicates an equally dramatic climate change coming out of the Younger Dryas, interpreted as a rapid increase in precipitation and/or temperature [80].

In East Africa, the most predominant response to this interval of rapid warming was ecological turnover and range adjustment. In the record from Lake Masoko [81], for example, a switch from forest dominated by taxa intolerant of a dry season to one containing species tolerant of a dry season occurred in less than 100 years at around 11 800 cal year BP (see the electronic supplementary material, figure S2). A similarly rapid turnover to climate warming is also seen in the palaeoecological record from Lake Kashiru in Burundi at this interval in time. Here, there was a switch from a grassland dominated ecosystem to woodlands [82] (see the electronic supplementary material, figure S2). Interestingly, at both sites, only a few local extinctions are noted associated with this rapid climatic transition. Instead, the main response was the rapid change in abundance of different taxa, a pattern similar to that seen throughout the Northern Hemisphere at this interval in time [76]. African plant species, at least in the regions studied thus far, appear to have had a level of tolerance and environmental plasticity to this interval of rapid climate change that enabled them to persist.

4. Discussion

The palaeoecological records presented here indicate some important additional factors that need to be taken into account when attempting to determine biotic response to future climate change; these are nonlinear features that will not necessarily be determined through modelling approaches alone, and can be summarized as follows.

First, there is a nonlinearity in the timing of the response of vegetation change to the same climatic driver. It would appear that slow climate trends can result in abrupt shifts in vegetation, and rapid climate changes may not incur rapid vegetation changes. For example, Tierney *et al.* [60] used paired compound-specific isotope records from the Holocene climate transition to show that major shifts in vegetation cover in the Tanganyika basin at 6.2–5.5 ka occurred during a time of only moderate drying. Prior to this, vegetation response was characteristically gradual, despite changes in wetness being typically abrupt [60]. This mismatch in the nature and timing of the relationship between climate variables and vegetation response is also noted in other regions of Africa [83]. Understanding this nonlinear behaviour is critical to understanding the level of confidence that can be placed in current and future predictions on the rate of response of African biota to climate change.

Second, there is nonlinearity in terms of the spatial response. In equatorial West Africa, for example, the interval of enhanced aridity between 4000 and 1000 cal year BP resulted in dramatic vegetation shifts from forest to savanna and to grassland in some areas, whereas other areas with the same climatic trigger saw little vegetation response. Reasons for these differences are important for determining spatial patterns of resilience across landscapes and, in particular, the sustainability of ecosystem service provision through time in response to climate change.

Third, there is nonlinearity in terms of the response of individual species and communities to climate change. In response to the AHP, for example, a large number of datasets from across West Africa indicate that while many woody species migrated north leading to the 'greening of the Sahara', they did so at individual rates and often following their own individual spatial trajectories, influenced by local topographical conditions [24,32,64]. Evidence for a large 'wave-like' biome movement in response to enhanced precipitation is totally lacking. These individual diffuse patterns of movement across landscapes in the fossil record, resulting in novel species assemblages and mosaic vegetation communities, provide a realistic representation of vegetation movement across the African landscape that could provide an important framework for future modelling studies.

All of the above is very important information for the current and future management of African landscapes because while at the broadest scale we might see extrinsic forcing leading to widespread turnover, the vast majority of evidence emerging from fossil records suggests that the rate and nature of this change is spatially highly variable and nonlinear. To date, palaeoecological data have provided qualitative information on the regional envelope of environmental variability for use in modelling [84], but it has enormous potential to be used in a quantitative sense to validate and hindcast models that project responses forwards into the future from the biome to the species scale [85]. The difficulty of obtaining the required lengthy, high temporal resolution data series that is required by such models may potentially be overcome by using combinations of high-resolution palaeoecological data and independent climate records during key periods analogous to forecast changes in climate.

Two other sources of information that are often not considered in modelling approaches but can be obtained from historical and palaeoecological records are the legacy of human impact and increasing atmospheric CO_2 concentrations on the African landscapes. Both have clearly had an impact and continue to have a significant impact on African biota, and the potential for using a longer-term perspective to obtaining information necessary for modelling of these two drivers will briefly be discussed in the following section.

Predicted future levels of anthropogenically induced atmospheric CO_2 indicate values ranging from 467 to 567 ppmv by 2050 and from 540 to 970 ppmv by the end of the twenty-first century. Ranges result from using different emission socio-economic scenarios [7,53]. Increasing CO_2 combined with warming affects photosynthesis and plant productivity, in what is known as the CO_2 fertilization process [76,86–88]. When the fertilization effect is implemented in dynamic vegetation models for future climatic scenarios, the output predicts enhanced plant growth, an increase in ecosystem productivity and higher diversity [89]. Historical records based on long-term monitoring plots, remote sensing and forest inventories largely agree with these predictions [90,91]. In the savanna biome of Southern and Eastern Africa, for example, historical photographs over the past 100 years indicate increased woody thickening of the savanna [13,92,93]. Evidence indicates that this thickening is due to the CO_2 fertilization process, through a mechanism of which fire survival and suppression is a key component [12,13,93–95]. Moreover, the observed increase in woody shrubs and trees in these savannas has involved a reduction of C_4 grasses in the understorey, implying fundamental changes of the species and functional assemblage of these communities [96]. This agrees with theorized increased competitiveness of trees and C_3 plants in general under increased atmospheric

CO_2 concentrations [97]. To add further support to this suggestion, *Acacia karroo* and *Terminalia sericea*, typical species of African savanna, were grown in growth chambers using a gradient of CO_2 treatments including that at the last glacial maximum (180 ppm) and above-ambient (450 ppm). In both species, as CO_2 concentration was increased, there was a significant increase in the mass of the root and shoot material [95].

Palaeoecological and historical records can also provide important additional information to understand impacts of future human activities upon the landscape. For example, changes in savanna fire regime of Southern Africa have been observed as a result of agro-pastoralism, especially in the past 4000 years, which may have potentially affected forest expansion [98]. In addition, in central West Africa, a recent study [99] has challenged the common belief that an arid event at around 2500 cal year BP caused a major decrease in forest [100–102], proposing instead that human land-use change was responsible for this vegetation change. Although this hypothesis remains under debate [103,104], it highlights the fact that more attention should be paid to past human impacts and their legacy on the current vegetation/climate of tropical Africa. This is a point often missed in modelling approaches and something that future studies should address when considering the relationship between vegetation and climate in Africa.

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