ORIGINAL ARTICLE

Towards an understanding of West African montane forest response to climate change

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ABSTRACT

Aim Our aims were to provide a detailed chronology of past vegetation changes in the tropical mountains of west-central Africa since the Last Glacial Maximum and to discuss montane forest responses to climate change in terms of distribution and biodiversity.

Location Lake Bambili, western Cameroon (05°56′ N, 10°14′ E, 2273 m a.s.l.).

Methods Fossil pollen was extracted from a long, continuous and well-dated sedimentary sequence extending back 20,000 years. Pollen diversity and evenness estimates were based on rarefaction analysis and on Simpson's ($1/D$) index.

Results Forest was nearly absent from high elevations during the last glacial period. It expanded gradually from 18.4 cal. kyr BP, interrupted only by reversals coincident with the Heinrich 1 (H1) and Younger Dryas (YD) climatic events, and then suddenly collapsed at 3.3 cal. kyr BP. This switch from forest to grassland communities occurred within a time span of three centuries. After 3.3 cal. kyr BP only short and taxon-poor forest phases are recorded, specifically between 2.7 and 1 cal. kyr BP and in recent centuries.

Main conclusions Our data indicate that the mountain forests of Cameroon are recent, resulting from plant migrations from various sources from 18.4 cal. kyr BP onwards. Their progressive development closely followed intensification of the Atlantic monsoon, leading to the formation of a dense forest between 11.7 and 3.3 cal. kyr BP. The composition of this forest included the co-occurrence of species whose ranges do not overlap today, and indicates the potential for the development of unique iterations of climax forests through time. These forests appear to be very sensitive to Northern Hemisphere climate change, with phases of expansion/contraction coeval with the boreal deglacial signal, including widely recognized events such as H1, the YD and the 8.2 ka event. From 8.2 cal. kyr BP onwards, the progressive opening of the canopy is likely to reflect increased seasonality in rainfall related to more frequent El Niño/Southern Oscillation (ENSO) events. The final step of this history was the collapse of the montane forest at 3.3 cal. kyr BP. During the last millennium, very severe disruptions have meant that only the most rapidly dispersing species could spread, contributing to a drastic loss of forest biodiversity that has been accentuated by human impact in the last few centuries.

Keywords
Africa, biodiversity, Cameroon, late Quaternary, montane forest, palaeoclimate, palynology, vegetation dynamics.

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Journal of Biogeography

INTRODUCTION

Tropical mountains are known to be both museums and cradles of biodiversity (Myers *et al.*, 2000). However, their high levels of biodiversity and endemism, resulting from diverse topography, steep environmental gradients and ecological isolation, are particularly vulnerable to the effects of habitat fragmentation by local anthropogenic activities and climate change (Lovett, 1993, 1999; Foster, 2001; Lomolino, 2001; Thuiller *et al.*, 2006). The highlands of the Cameroon Volcanic Line (CVL) in west-central Africa are considered to be 'hotspots' of biodiversity (Myers *et al.*, 2000). They include numerous endemic species such as *Schefflera mannii* and *Myrica arborea*, both of which are considered vulnerable (Cheek, 2004a, b). Some other forest elements (e.g. *Podocarpus latifolius*, *Prunus africana*) are also found in the eastern African highlands, and their presence may be the result of east–west migrations during glacial periods (e.g. White, 1993; Kadu *et al.*, 2011). The biological response of these complex ecosystems to past climate change is poorly understood, particularly because of the lack of long-term, high-resolution archives. Unlike the situation for eastern Africa mountains, where numerous long and high-resolution pollen sequences have been produced (e.g. Bonnefille *et al.*, 1995; Wooler *et al.*, 2003; Mumbi *et al.*, 2008; Finch *et al.*, 2009), there are no pollen records from the mountains of Atlantic central Africa. The only existing pollen records are from low to mid-elevations (e.g. Assi-Kaudjhis *et al.*, 2010, and references therein) with only one, Lake Barombi Mbo (Maley & Brenac, 1998; Lebamba *et al.*, 2012), providing a continuous sequence including part of the last glacial period.

However, the CVL hosts numerous crater lakes and peat bogs, which – as a result of their small drained areas and high deposition rates – are potentially valuable archives that can produce long sedimentary records, and thus elucidate patterns of long-term variability in the mountain vegetation. Thus, the CVL is a key region for the study of the vegetation response to climate change at high elevations. Diatom analyses by Stager & Anfang-Sutter (1999) at Lake Bambili have suggested that the lacustrine environment experienced high-amplitude fluctuations, probably linked to climate. Owing to the scarcity of dated archaeological evidence in the area, a link with human activity is difficult to establish, even though we know that the region has been inhabited since 30 cal. kyr BP (e.g. Asombang, 1998), with the exception of the last century when Fulbe pastoralists entered the Bamenda plateau (Boutrais, 1981).

In this paper, we present pollen data from a continuous 20,000-year-long sedimentary sequence recovered from the edge of Lake Bambili, the first – and so far only – high-resolution record of mountain forest history in Atlantic central Africa. While the representativeness of these results remains to be established by other records in the same area, they allow discussion of (1) the link between environmental stability over time and present-day floristic diversity, including the origin of the present-day montane forest, and (2) the

sensitivity and response of montane forest to climate change. Particular attention will be given to the last glacial period in order to evaluate the behaviour of the main montane trees and the so-called 'refuge theory' (White, 1993), and to the end of the African Humid Period (AHP) (deMenocal *et al.*, 2000) to discuss the abrupt collapse of the forest and possible causes of this major environmental change.

STUDY SITE

Lake Bambili (5°56′11.9″ N, 10°14′31.6″ E, 2273 m a.s.l.) is a shallow 16.5-ha crater lake with a mean depth of 4 m located between the Bamenda Plateau and the Bambutos Mountains (Fig. 1). In this region, vegetation currently displays an elevational distribution (Letouzey, 1968, 1985; Cheek *et al.*, 2000; Harvey *et al.*, 2004), which has been highly disturbed by grazing, fire and human activities (Momo Solefack, 2009; Assi-Kaudjhis, 2011). Between roughly 1200 and 2000 m a.s.l., mid-elevation savanna (*Annona senegalensis*, *Bridelia ferruginea*, *Cussonia djalonensis*, *Terminalia avicennioides*, *Hymenocardia acida*, *Protea madiensis*) and sub-montane forest (*Celtis* spp., *Clausena anisata*, *Alchornea laxiflora*, *Macaranga occidentalis* and *Ficus* spp.) occur. The floristic composition of sub-montane forest does not differ strongly from that of low-elevation semi-deciduous forest. It has thus been included by White (1983) within the Guineo-Congolian phytogeographical region. Between 2000 and 2800 m a.s.l., forests from the Afromontane regional centre of endemism (White, 1983) have characteristic mountain trees such as *Schefflera* spp. (1800–2300 m a.s.l.), *Syzygium staudtii* (1900–2500 m a.s.l.), *Podocarpus latifolius* (2000–2800 m a.s.l.), *Embelia* spp. (2200–2650 m a.s.l.), *Nuxia congesta* (2300–2500 m a.s.l.), *Prunus africana* (2300–2800 m a.s.l.), *Maesa lanceolata* (2300–2800 m a.s.l.) and *Rapanea melanophloeos* (2400–2800 m a.s.l.) locally associated with *Ficus* spp. (1400–2300 m a.s.l.), *Acalypha* spp. (2000–2100 m a.s.l.) and *Olea capensis* (2000–2300 m a.s.l.). At the edges of the forest or in forest gaps, light-demanding shrubs and trees such as *Gnidia glauca* (1900–2900 m a.s.l.), *Hypericum* spp. (2000–2900 m a.s.l.) and *Ilex mitis* (2100 m a.s.l.) occur. Above 2800 m a.s.l., Afro-alpine vegetation (White, 1983) consists mainly of ericaceous shrublands (*Erica* spp.) at the upper tree line followed, towards the top of the mountains, by grasslands with numerous specimens of *Alchemilla* and Poaceae. In contrast to the situation in east Africa, *Artemisia afra*, which is considered as a marker of very high elevations (Beentje, 2002), has never been found in the CVL.

Lake Bambili lies in the Afromontane forest belt. Large patches of forest occur on the crater slopes, with the main arboreal components being *Schefflera mannii*, *Schefflera abyssinica*, *Syzygium staudtii*, *Rapanea melanophloeos*, *Maesa lanceolata*, *Carapa procera*, *Trilepisium madagascariensis* and *Sinarundinaria alpina*, associated with *Gnidia glauca* and *Hypericum* spp. at the lake shore. *Olea capensis* and *Podocarpus latifolius* are absent; their nearest populations are
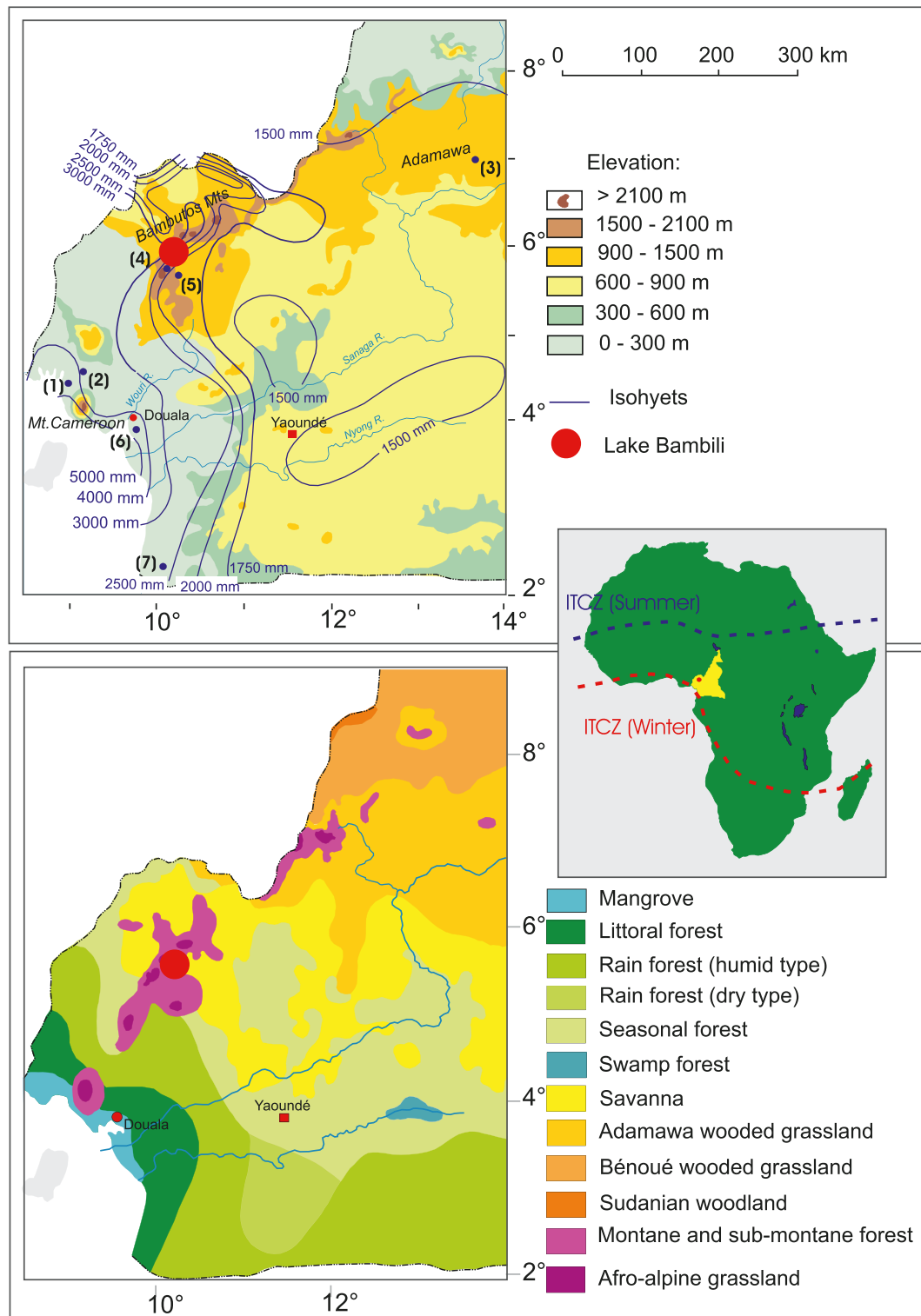
Figure 1 Location map of Lake Bambili in Cameroon. The upper panel shows the distribution of mean annual rainfall. The lower panel shows the distribution of the vegetation. The Inter-tropical Convergence Zone (ITCZ) position is from Shanahan *et al.* (2006). Pollen sites in Cameroon: 1, Barombi Mbo; 2, Mboandong; 3, Mbalang; 4, Shum Laka; 5, Bafounda; 6, Ossa; 7, Nyabessam.

found on Mount Oku, *c.* 40 km to the north (Letouzey, 1968, 1985; Momo Solefack, 2009).

Owing to the distance from the coast (about 250 km), the direct climatic influence of the Atlantic Ocean is attenu-

ated (Suchel, 1988), and annual precipitation at Bambili averages 2000 mm, with peaks in March–April and July–September. Monthly rainfall can reach 400 mm. Rains are intense and regularly distributed, with 5 months above

200 mm, and mists are frequent during the rainy season. The dry season lasts from November to February, with monthly rainfall less than 50 mm. The monthly average temperature does not exceed 18 °C and is relatively constant during the year (Hijmans *et al.*, 2005). Frost occurs only occasionally.

MATERIALS AND METHODS

Our pollen record was obtained from a 14-m-long composite core of overlapping sections (5 cm in diameter and 60 cm in length) retrieved at the northern lakeshore. The cores were recovered from two sites within 2 m distance using a manual 'Russian' peat corer (Jowsey, 1966). The sediments consist of organic-rich clay and peat. The average sedimentation rate is 0.05 mm year^{-1} from the base to 699 cm, and 0.208 mm year^{-1} from 699 cm to the top, supporting a comprehensive age-model chronology based on linear interpolation between successive dated levels. Eighteen accelerator mass spectrometry radiocarbon dates on plant macro-remains and charcoal were obtained. Calibration of radiocarbon dates into calendar age was done using the software CALIB 5.0.1 (Stuiver & Reimer, 1993) and IntCal04 data (Reimer *et al.*, 2004) (see Appendix S1 in Supporting Information). On the basis of this chronological framework, the Lake Bambili pollen sequence is continuous and extends back 20,000 years (20 cal. kyr BP).

Samples (155, 0.5 cm^3 each) were taken at 5–10 cm intervals throughout the whole sedimentary sequence for pollen studies, corresponding to an average time resolution of 126 years. Samples were processed using standard hydrofluoric acid methods (Faegri & Iversen, 1975). A total of 196 pollen and fern taxa were determined (see Appendix S2) for a pollen count ranging from 203 to 1469, the highest counts being performed in samples in which one or two taxa were strongly predominant. Following standard palynological practices, pollen types from aquatic and lake-shore plant communities were excluded from calculation of the sum for terrestrial taxa percentages (Figs 2 & 3) and for the richness and evenness analyses (Fig. 5). Based on major fluctuations in the microfloristic composition, pollen zones were drawn using constrained cluster analysis by sum of squares using the program TILIA (Grimm, 1987).

Pollen-based diversity estimates were calculated using rarefaction analysis (Birks & Line, 1992), which estimates pollen richness by standardizing the pollen count. Here, the minimum count was 90. To complement this, Simpson's index of diversity ($1/D$) was used to estimate pollen evenness, that is, the distribution of species abundance (Smith & Wilson, 1996; Peros & Gajewski, 2008). Compared with the other indices generally used in palaeoecology, $1/D$ is thought to be less affected by pollen richness and only slightly affected by sample size. It is, moreover, sensitive to density variations of 'rare' taxa (Gelorini, 2011).
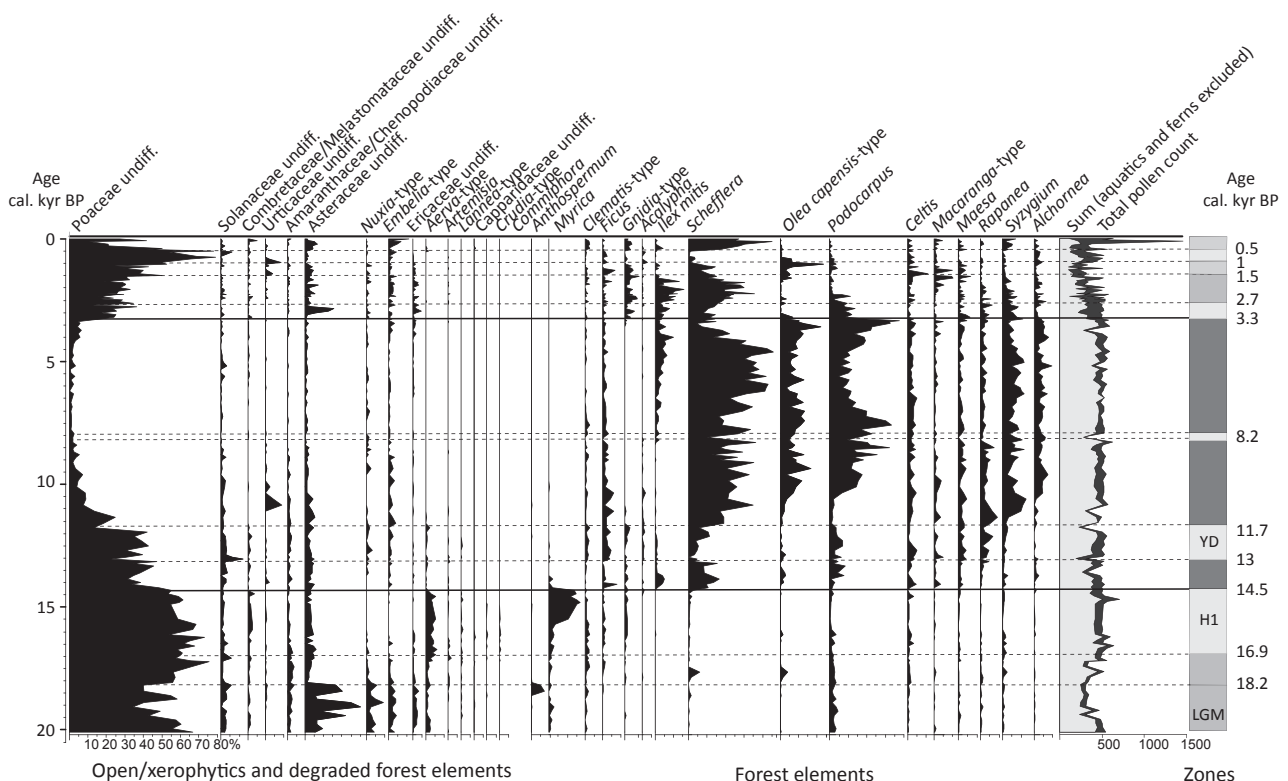
Figure 2 Lake Bambili (Cameroon) summary pollen diagram showing percentages of selected pollen types over time. (Percentages of taxa are calculated on the sum of pollen from terrestrial plants, excluding those from aquatic and lake-shore plant communities.) LGM, Last Glacial Maximum; H1, Heinrich 1 event; YD, Younger Dryas event.
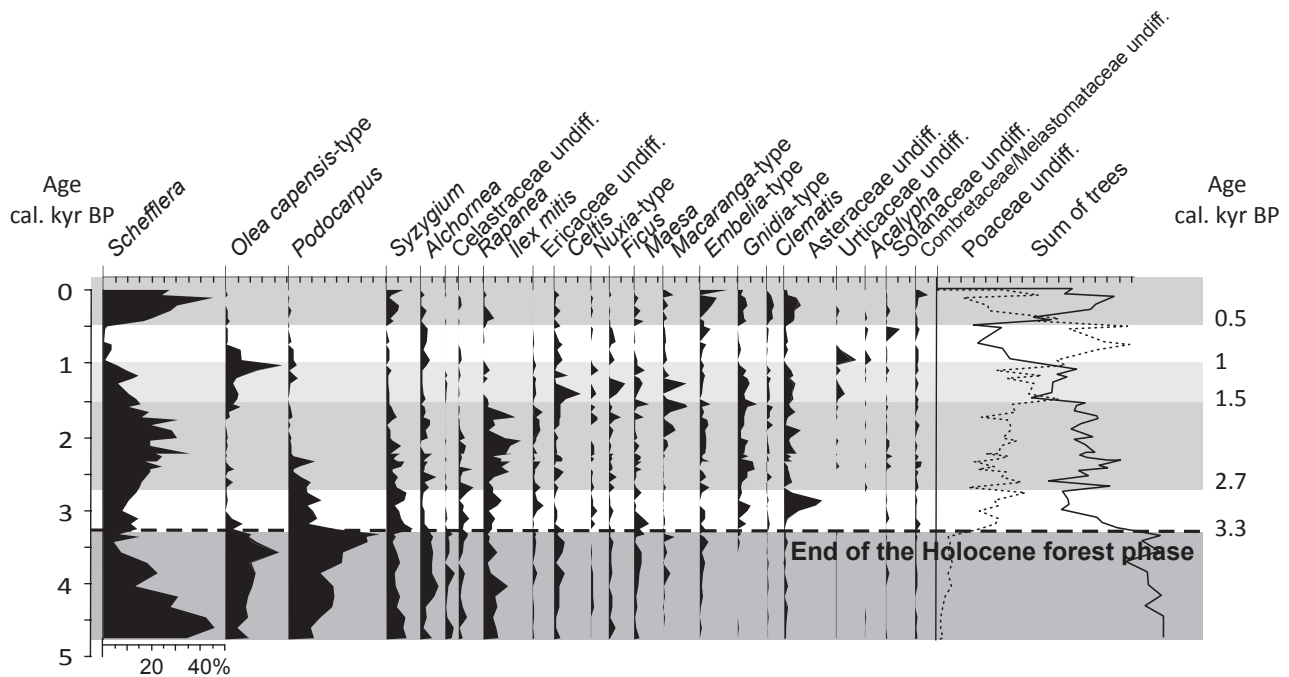
Figure 3 The end of the forest phase at Lake Bambili (Cameroon). Details of the main pollen types are shown. The grey bands show the successive forest phases.
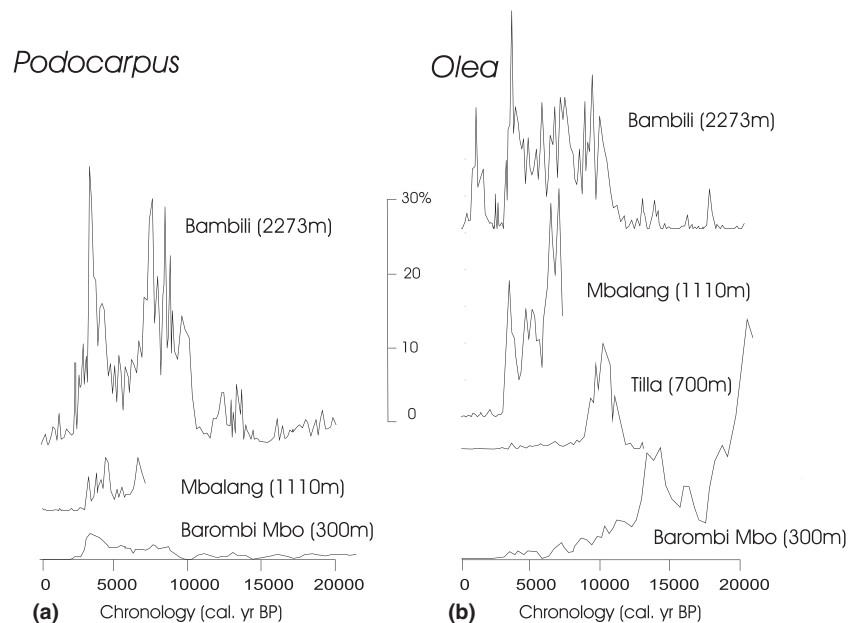
Figure 4 Behaviour of two montane plant types, (a) *Podocarpus* and (b) *Olea*, during the last 20,000 years in major pollen sites of west-central Africa. Data from Bafounda (Cameroon) and the Batéké plateau (Congo) are not shown due to the lack of an accurate age model at these sites.

RESULTS

The end of the last glacial period (20–18.2 cal. kyr BP)

A period of open vegetation is recorded at the base of the pollen sequence (Fig. 2). It is characterized by maximum values of herbaceous taxa, mainly Poaceae and Asteraceae, associated with various Solanaceae and Amaranthaceae/Chenopodiaceae. Pollen of montane tree and shrub populations occur: mainly *Nuxia*, associated with *Embelia*, *Podocarpus* and various Ericaceae. However, their very low values (4%, 5%, 2% and 3%, respectively) record the extreme contraction of the forest tree cover in the immediate surroundings of Lake Bambili at this time, and/or the distance of the source plants from the site. Surprisingly,

during this time interval, pollen grains of plants characteristic of lowland steppes (e.g. *Aerva/Cornulaca* and *Artemisia*, the latter classified as steppic according to its absence in the flora of the western Cameroon Highlands today) and of wooded grasslands (*Lannea*, *Commiphora* and various Capparidaceae), today found north of the Adamawa plateau in Cameroon about 350 km to the north-east, are present, some of them with significant percentages (e.g. *Aerva/Cornulaca*: maximum 6%). The composition of the pollen spectra between 20 and 18.2 cal. kyr BP does not correspond to any known modern assemblages, owing to mixtures of taxa that today occupy distinct ecosystems. The high abundances of herbaceous taxa suggest that regional dry climatic conditions prevailed at both high and low elevations. Thus, the widespread dryland expansion, linked to the enhanced anti-cyclonic circulation intensity recorded in western Africa during the last glacial period (e.g. Sarnthein *et al.*, 1981), was also perceptible at high elevations in the CVL. Intense north to north-east dry wind circulation has played a role in transporting pollen grains from lowland xerophytic plant populations, but we have no direct evidence of a lowering of temperature as previously claimed by Farrera *et al.* (1999) for equatorial Africa. Our results agree with the interpretations of Jolly & Haxeltine (1997) and Wu *et al.* (2007) that low precipitation, associated with low CO_2, was a primary determinant of plant distribution in equatorial mountains during the LGM. The absence of typical Afro-alpine taxa such as *Alchemilla*, which today grows at the tops of the mountains, means that the lowering of the Afro-alpine vegetation belt by

1000 m observed in eastern Africa (e.g. Jolly & Haxeltine, 1997, and references therein) is not evident at Bambili.

The last glacial–interglacial transition (18.2–12 cal. kyr BP)

The first evidence of forest expansion at Bambili dates from 18.4 cal. kyr BP with the appearance of *Anthospermum*. According to Livingstone (1967), this subshrub is an important element of the early colonizing stage on lava fields in the volcanic region of the Virunga Mountains in East Africa. *Anthospermum* was immediately followed by the first discrete increase of two montane forest elements – *Olea* and *Schefflera* – at 17.6 cal. kyr BP. The expansion of these genera was interrupted from 16.9 to 14.5 cal. kyr BP, a period corresponding within dating errors to the widespread episode of intense drought throughout the tropics synchronous with the global climate cold 'Heinrich event 1' (H1) (e.g. Stager *et al.*, 2002) that originated in the North Atlantic basin (Stanford *et al.*, 2011). This event is characterized at Bambili mainly by the minimum arboreal pollen (AP) percentages (9.5%) and the high values of *Aerva/Cornulaca* (4.3%), which suggest a dramatic increase in dry conditions. Forest colonization restarted at 15.5 cal. kyr BP with an increase in *Myrica* pollen. The expansion of this fire-resistant, shade-intolerant and active pioneer tree (Cheek, 2004b) was immediately followed by that of another shade-intolerant species, *Ilex mitis*, at 13.9 cal. kyr BP, and then by the typical montane forest trees *Olea*, *Podocarpus* and *Schefflera* at 13.7 cal. kyr BP. Forest colonization continued into the early Holocene, interrupted *c.* 12.9 cal. kyr BP during the Younger Dryas (YD), another episode of global climate disruption (Alley, 2000). Forest contraction during this event (with total AP falling from 48% to 29%) mainly affected *Schefflera*, while minor taxa such as *Maesa*, *Rapanea*, *Nuxia*, *Embelia* and *Gnidia* continued to increase. The continuous presence of pollen of the light-demanding genus *Gnidia*, most probably *Gnidia glauca*, between 18.4 and 12 cal. kyr BP, associated with *Acalypha*, common on forest borders from 14.3 cal. kyr BP onwards, demonstrates the opening of the forest all through this period, and particularly during the YD. Similarly, the presence – albeit at low percentages and with scattered occurrences – of pollen from lowland steppes and wooded grasslands suggests the persistence of anti-cyclonic circulation intensity and the north to north-east dry wind circulation already in evidence at the end of the glacial period.

The Holocene Humid Period (11.7–3.3 cal. kyr BP)

The period 11.7–8.3 cal. kyr BP

Montane forest taxa, mainly *Schefflera*, *Ficus* and *Rapanea*, progressively increased from 11.7 cal. kyr BP onwards. After 10 cal. kyr BP, they were associated mainly with *Syzygium*, *Olea* and *Podocarpus* to form the 'Bambili forest optimum' (10–8.3 cal. kyr BP). During the 'Bambili forest optimum',
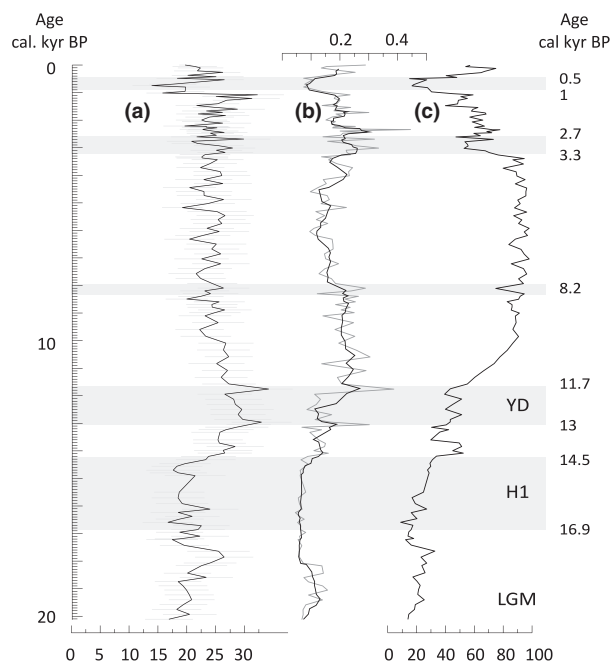
Figure 5 Temporal changes in diversity at Bambili (Cameroon) during the last 20,000 years: (a) rarefaction analyses for richness estimates, (b) 1/*D*, Simpson's index of diversity for evenness estimates, with the curve of two sample running mean values (in black), (c) AP, arboreal pollen percentages.

percentages reached by the mountain tree taxa are among the highest in the entire sequence. Euphorbiaceae, mainly *Alchornea* and *Macaranga*, which are currently restricted to lower elevations in the sub-montane vegetation belt, were also abundant. Together with the presence of other light-dependent taxa such as *Maesa*, their abundance suggests that the canopy was not fully closed, a pattern generally observed in gymnosperm forests today (Lebrun & Gilbert, 1954). AP percentages averaged 87%, whereas herbaceous taxa, mainly Poaceae, decreased to their lowest pollen values. At the same time, pollen grains from dry lowland vegetation disappeared, indicating a change in wind direction and/or the expansion of forests caused by the northward migration of the monsoon front during the early Holocene (Watrin *et al.*, 2009).

The 8.2 ka event?

At 8.3–8.1 cal. kyr BP, a marked fall in AP percentages interrupted the Holocene forest phase, with values (73%) significantly lower than at any other time during this period. This fall corresponded mainly to a decline in the main montane forest taxa: *Podocarpus*, *Olea* and *Rapanea*. At the same time, *Ilex mitis*, which was absent during the previous forest phase, reappeared. This suggests a brief signal of forest clearance, allowing the growth of light-dependent trees. However, the opening of the canopy was not extensive enough to permit the expansion of grasses. This episode lies within the time interval of the '8.2 ka' cold event of northern latitudes (von Grafenstein *et al.*, 1997), during which dry conditions widely expanded throughout the tropics (Gasse, 2000).

The period 8.1–3.3 cal. kyr BP

This period is typified by the progressive increase of *Ilex mitis*. The composition of the forest remained otherwise unchanged compared with the early Holocene forest optimum, with three main taxa: *Schefflera*, *Podocarpus* and *Olea*. *Schefflera* and *Podocarpus* display opposite trends to which we are unable, in the present state of our knowledge, to assign any ecological/climatic significance. The highly variable representation of these taxa, reflected in AP percentages that vary between 77.5% and 95.2%, together with the progressive increase of *Ilex mitis* provide evidence for the instability of the forested environment during the mid-Holocene.

The three last millennia (3.3 cal. kyr BP–present)

A dramatic fall in AP percentages marks the end of the Holocene forest phase. This fall took place over a time span of only 300 years, with pollen representation of forest cover (AP) decreasing by 40% between 3.3 and 3.0 cal. kyr BP, when Poaceae abruptly increased. At the same time, the sedimentation rate increased, suggesting an increase in soil erosion linked to the degradation of the forest cover (see Appendix S1) (Bayon *et al.*, 2012). This collapse did not result in the concomitant disappearance of all forest components, but in the successive, more or less abrupt, decline of the main arboreal pollen taxa from 4.3 cal. kyr BP onwards (Fig. 3). Between 4.3 and 3.3 cal. kyr BP, however, the dramatic fall of *Schefflera* was largely counterbalanced by the other forest elements: *Olea* and *Podocarpus*, associated with *Alchornea*, *Macaranga*, *Celtis* and *Ilex* – all typically light-dependent taxa. From 2.7 to 1.5 cal. kyr BP, a minor forest phase was dominated by *Schefflera* associated with *Ilex mitis*, *Gnidia*, *Embelia*, and then Ericaceae. *Podocarpus* strongly decreased, indicating its final retreat from the Lake Bambili area beginning 3.3 cal. kyr BP. From 1.5 to 1 cal. kyr BP, *Schefflera* decreased, whereas *Olea*, *Macaranga*, *Celtis*, *Maesa*, *Nuxia*, *Gnidia* and *Ficus* all increased. From 0.5 cal. kyr BP to the present, few arboreal taxa were present: mainly *Schefflera*, *Embelia*, *Syzygium* and *Gnidia* associated with *Clematis*. The sharp increases of Poaceae, Urticaceae, Solanaceae and Asteraceae at 3.3–2.6 cal. kyr BP, 1.4 cal. kyr BP, and particularly 0.7–0.5 cal. kyr BP, illustrate phases of more or less accentuated forest disruption.

Temporal changes in diversity

At Bambili, the period of highest floristic richness is recorded during the YD between 13 and 11.7 cal. kyr BP (Fig. 5). Minor phases of floristic richness are also recorded at 18.5–17.5 cal. kyr BP and during the late Holocene around 1 cal. kyr BP. In contrast, the end of the Last Glacial Maximum (LGM; *c.* 24–19 cal. kyr BP), H1 (*c.* 15.5 cal. kyr BP) and the period centred at 0.7 cal. kyr BP are characterized by dramatic decreases in diversity. At these times, pollen taxa are also less evenly distributed. This evidence is consistent with episodes of marked forest contraction. However, a long period of evenly distributed taxa (i.e. the highest $1/D$ values) is reported during the post-glacial forest colonization and the subsequent forest optimum (11.8–8.2 cal. kyr BP), illustrating the post-glacial expansion of taxa. Evenness values decreased during the mid-Holocene (8.3–3.3 cal. kyr BP), which is consistent with the instability of the forested environment described above. The end-Holocene period, between 3.3 and 1 cal. kyr BP, appears to have been highly variable, reflecting the complexity of the forest history after 3.3 cal. kyr BP.

DISCUSSION

Vegetation dynamics and biodiversity

Was the Bambili site a 'glacial forest refuge'?

The mechanisms behind evolutionary diversification in African rain forests are still a matter of debate. Most studies have focused on the Amazon and Australian wet tropics, and data from central Africa remain relatively rare (see Anthony *et al.*, 2007, and references therein). Numerous hypotheses have been proposed, of which the Pleistocene forest refuge hypothesis has long provoked considerable interest (Hamilton, 1982). According to this, forest fragmentation during glacial periods led to the isolation of forest taxa. Then, during periods of

climate amelioration and population expansion, zones of secondary contact may have formed between neighbouring refugial populations. Hence, long-term environmental stability is thought to be the main factor responsible for the accumulation and persistence of species over time, thus resulting in the high diversity observed today in tropical 'hotspots of biodiversity' (Myers *et al.*, 2000). New pollen analyses carried out in the uplands of the Uluguru Mountains (Mumbi *et al.*, 2008; Finch *et al.*, 2009) in the Eastern Arc Mountains – one of these 'hotspots of diversity' (Lovett, 1993) – corroborate the above assumption by showing no substantial environmental change during the last 48 kyr. However, pollen data from other mountain regions also defined as 'hotspots of biodiversity' and/or 'glacial forest refuges' (Hamilton, 1982; Myers *et al.*, 2000), such as the CVL (Bambili, this study) or the Kivu Mountains at the eastern border of the Guineo-Congolian forest (Rusaka – 2070 m a.s.l.; Bonnefille *et al.*, 1995), show a clearly different pattern with high-amplitude environmental changes since 20 cal. kyr BP. The very low percentages and scattered occurrence of all the arboreal taxa at the end of the last glacial period, combined with high percentages of herbaceous taxa (mainly Poaceae) at both sites, suggest that the forest was locally sparse, if not absent. In consequence, Bambili and Rusaka cannot be designated as 'glacial forest refuges', unlike the Uluguru sites. The different environmental histories displayed in all these mountain sites in tropical Africa suggest that the link between environmental stability and biodiversity is not necessarily a rule.

Based on pollen analyses that suggested that Afromontane tree populations have tended towards lower elevations during the last glacial period and part of the Holocene (e.g. Elenga *et al.*, 1991), White (1993) proposed an alternative hypothesis in which Afromontane forests can be considered relicts occupying refuges in response to exceptionally favourable conditions that date only to the relatively recent past. They may thus be vulnerable to ongoing climate change.

Range shifts during the last glacial–interglacial transition and the Holocene

Time series comparable to that of Lake Bambili are extremely rare in west-central Africa, considerably limiting the discussion of White's (1993) hypothesis. Nevertheless, comparisons with nearby pollen sequences, mainly Barombi Mbo (Maley & Brenac, 1998), Tilla (Salzmann *et al.*, 2002) and Mbalang (Vincens *et al.*, 2010), give some insights into plant responses to climate change at the last glacial–deglacial transition in mountain areas. In particular, they allow discussion of the timing and amplitude of shifts in elevation for the two main components of the Afromontane forest: *Podocarpus* and *Olea* (Fig. 4).

The presence of *Podocarpus* is demonstrated at Shum Laka (1355 m a.s.l.: Kadomura & Kiyonaga, 1994) on the Bamenda plateau during the last glacial period from a single level dated *c.* 28.8 cal. kyr BP and also from much farther south,

on the Batéké plateau in Congo (600 m a.s.l.: Elenga *et al.*, 1991), *c.* 13 cal. kyr BP. At both sites, *Podocarpus* pollen percentages reach high values (17% and 30%, respectively), suggesting the local presence of the parent trees. During the Holocene, however, *Podocarpus* seems to have been restricted to the Bamenda plateau and the nearby mountains, as indicated by its high pollen percentages (30% or more) recorded at Bafounda (1400 m a.s.l.: Tamura, 1990) and at Bambili (this study). At lower elevations, however, in the Adamawa plateau (Mbalang – 1100 m a.s.l.: Vincens *et al.*, 2010) and in the lowland forest sites (Ossa – 8 m a.s.l.; Reynaud-Farrera *et al.*, 1996; Barombi Mbo – 300 m a.s.l.: Maley & Brenac, 1998; Lebamba *et al.*, 2012; Mboandong – 100 m a.s.l.: Richards, 1986), its values of consistently less than 10% indicate the distant location of the parent trees. We speculate that during the last glacial, *Podocarpus* populations were restricted to favourable climates that were located at middle elevations (Fig. 4a). They then moved towards higher elevations at the beginning of the Holocene. At Bambili, two main phases of *Podocarpus* increase are recorded, between 10 and 7 cal. kyr BP, and between 4.5 and 3.3 cal. kyr BP. The onset of the latter is synchronous with the expansion of gymnosperm forests in east Africa north of the equator as a result of increased rainfall seasonality (e.g. Vincens *et al.*, 1986).

The other main component of the montane forest, *Olea*, displays a different pattern (Fig. 4b). During the last glacial period, *Olea* occurred in the lowlands near Lake Barombi Mbo (Maley & Brenac, 1998). Here, *Olea* pollen abundance reaches about 30% at levels dated from *c.* 20 cal. kyr BP, then regularly decreases from 12 cal. kyr BP onwards. This taxon is also found northwards at Tilla (700 m a.s.l.: Salzmann *et al.*, 2002), where it dominates the earliest stage of the postglacial forest colonization between 11.5 and 9.5 cal. kyr BP, and finally at Bambili (2200 m a.s.l.), where it increases only after 10.3 cal. kyr BP. *Olea* is also found at high percentages at Mbalang, showing that the parent trees expanded widely on the Adamawa plateau during the Holocene.

During the Holocene, some of the taxa, mainly *Alchornea* and *Celtis*, that now grow at lower elevations in the submontane and lowland forests were present at Bambili in association with the Afromontane forest taxa. Today, their highest elevations in Cameroon do not exceed 1300 m and 1420 m a.s.l., respectively (Letouzey, 1968; Harvey *et al.*, 2004). They are abundant pollen producers, and their pollen grains can be found in modern samples outside the range of the plant. When grains occur in proportions of less than 2%, they can typically be identified as originating from long-distance transport (Watrin *et al.*, 2007). *Alchornea* and *Celtis* pollen exceptionally reach up to 10% and 11%, and average 4% between 10 and 1.7 cal. kyr BP (*Alchornea*) and 3% between 10 and 3.2 cal. kyr BP (*Celtis*). These values suggest the local presence of the parent trees, even in small numbers, during the Holocene. The upward distribution of *Celtis* and *Alchornea* during the Holocene has already been detected in the eastern African mountains, in Uganda (Kitandara – 3990 m a.s.l. and Mahoma – 2960 m a.s.l.: Livingstone, 1967) and in Burundi

(Kuruyange – 2000 m a.s.l.: Bonnefille *et al.*, 1991; Jolly *et al.*, 1994; Kashiru – 2240 m a.s.l.: Bonnefille & Riollet, 1988; Rusaka – 2070 m a.s.l.: Bonnefille *et al.*, 1995). Which climate parameters allowed the co-occurrence of species whose ranges do not overlap today is still an unresolved question. However, as stated by Bonnefille & Riollet (1988), during the Holocene 'many inter-vegetation community changes took place, and the fact that the plant species were formerly sorted into different communities cannot be excluded'. All these examples confirm that the patterns of migration during the past 20 kyr have been idiosyncratic and have not merely involved elevational displacement of the existing vegetation belts (Davis & Shaw, 2001).

Vegetation and climate

The last glacial–deglacial transition

Several forcing factors may explain the vegetation history at Bambili (Fig. 6). The role of summer insolation in controlling the

African monsoon is now well established (e.g. Marzin & Braconnot, 2009), with an insolation maximum corresponding to maximum rainfall over tropical Africa. The transition from arid (glacial) to humid (Holocene) climate occurred between 18.5 and 15.5 cal. kyr BP in west-central Africa, as recorded by the rise of lake level at Lake Bosumtwi (Shanahan *et al.*, 2006), the increase of fluvial activity in the Gulf of Guinea (Lézine *et al.*, 2005; Weldeab *et al.*, 2007; Kim *et al.*, 2010; Sangen *et al.*, 2011) and forest expansion in the equatorial lowlands (Maley & Brenac, 1998; Lebamba *et al.*, 2012). This timing matches the Bambili record, which shows that the local forest was extremely reduced during the terminal last glacial period, and started to expand in two steps dated at 18.4 and 15.5 cal. kyr BP to reach its maximum ('the Bambili forest optimum') between 10.5 and 8.3 cal. kyr BP. The forest expansion was punctuated by phases of more or less pronounced contraction, the timing of which suggest millennial-scale climate fluctuations superimposed on the long-term insolation forcing. These phases fall within the H1, YD and
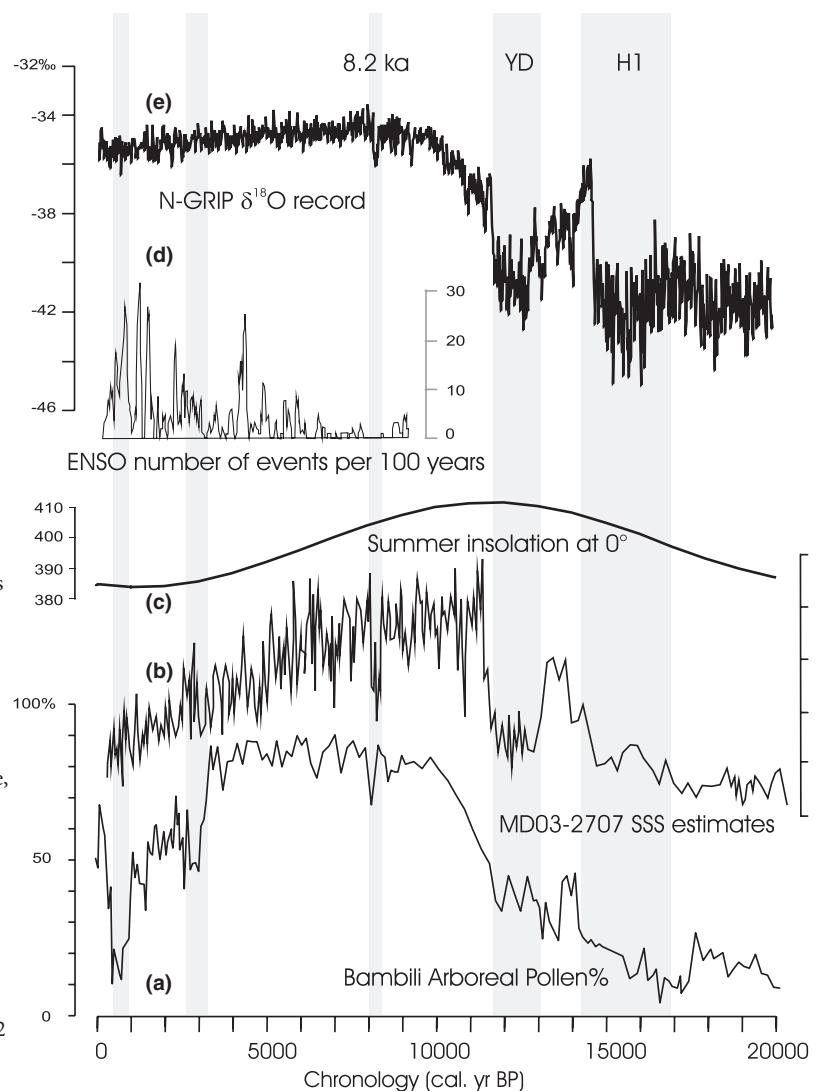
Figure 6 Lake Bambili vegetation history and climate. (a) The Bambili arboreal pollen curve closely matches with proxies of (b) monsoon rainfall fluctuations in the Gulf of Guinea [marine core MD03-2707 sea surface estimates calculated using $\delta^{18}O$ of sea water (sw)–sea surface temperature (SST)–sea surface salinity (SSS) relationship for eastern low latitude Atlantic; Weldeab *et al.*, 2007] and (e) Northern Hemisphere climate (N-GRIP $\delta^{18}O$ record; North Greenland Ice Core Project members, 2004). (d) During the late Holocene, the abrupt vegetation response contrasts with the orbitally induced gradual decrease in precipitation in the Gulf of Guinea as a possible consequence of increased seasonality linked to more frequent El Niño/Southern Oscillation (ENSO) events since the mid-Holocene (Moy *et al.*, 2002). (c) The curve of summer insolation at 0° (W m^{-2}) is from Berger & Loutre (1991). The timing of the '8.2 ka', 'Heinrich 1' (H1) and 'Younger Dryas' (YD) climatic events is also shown.

8.2 ka intervals of northern latitudes as recorded by the $\delta^{18}O$ N-GRIP record (North Greenland Ice Core Project members, 2004), which points to strong teleconnections between monsoonal and high-latitude climate systems. The mechanisms behind this millennial-scale variability are likely to be tied, according to Cheng *et al.* (2009) and Stanford *et al.* (2011) among others, to changes in the Atlantic Meridional Overturning Circulation (AMOC) triggered by freshwater discharges in the North Atlantic. These may have affected the tropical Atlantic Ocean, the monsoon system, and the mean latitudinal position of the Inter-tropical Convergence Zone (ITCZ).

The end of the Holocene forest phase

The forest collapse recorded at 3.3 cal. kyr BP at Bambili falls within the general context of the end of the AHP (deMenocal *et al.*, 2000), which was characterized by a series of large-amplitude environmental changes (Vincens *et al.*, 1999; Marchant & Hooghiemstra, 2004; Kröpelin *et al.*, 2008). Rainfall has decreased since the mid-Holocene, as shown by the gradual decrease of fluvial activity in the Gulf of Guinea (e.g. Lézine *et al.*, 2005; Weldeab *et al.*, 2007; Itambi *et al.*, 2010), while rainfall seasonality has increased, with seasonal forests expanding at the northern edge of the forest (Lézine & Vergnaud-Grazzini, 1993). On land, a complex situation is observed (Lézine, 2007), which corresponds to what Williams *et al.* (2011) define as a 'temporal mosaic of site-level response to regional aridification': lakes dried out, for example Sinnda (4.7–4.6 cal. kyr BP; Vincens *et al.*, 1998), or recorded low levels, for example Bosumtwi (4.3–2.8 cal. kyr BP; Shanahan *et al.*, 2006). As already shown by Vincens *et al.* (1999), the signature of this climate deterioration on the forest vegetation was site-dependent, mainly as a result of local hydro-geological conditions. Some sites remained forested (Bosumtwi: Talbot *et al.*, 1984; Barombi Mbo: Maley & Brenac, 1998; Lebamba *et al.*, 2012), while others were partially affected, with rain or swamp forests being replaced by more open formations with an increasing importance of light-dependent trees (e.g. Ossa: Reynaud-Farrera *et al.*, 1996; Nyabessam: Ngomanda *et al.*, 2009). Forests also disappeared from the Adamawa plateau to the north (Lake Mbalang: Vincens *et al.*, 2010) as open and dry ecosystems expanded widely throughout the Sudanian vegetation zone (Salzmann *et al.*, 2002), the Sahel (Lézine, 1988, 1989; Salzmann & Waller, 1998) and the Sahara (Lézine *et al.*, 2011). The 'Dry Dahomey Gap', which interrupts the Guineo-Congolian forest domain in Benin/Togo, dates from the same period (Salzmann & Hoelzmann, 2005).

At Bambili, the forest collapse lagged seven centuries behind the onset of this period of widespread aridity. A hypothesis of critical thresholds (so-called 'tipping points': Scheffer *et al.*, 2001; Drake & Griffen, 2010) with abrupt forest contraction emerged from studies of sub-Guinean forests in Senegal (Lézine, 1988, 1989), but studies in semi-deciduous forests of west-central Africa (Runge, 2002; Vin-

cens *et al.*, 2010) suggested a longer process characterized by successive discrete phases of forest contraction–expansion during the mid-Holocene. Such fluctuations were not recorded at Bambili, where the forest cover remained dominant throughout the AHP. Its composition, however, appears to have been increasingly variable compared with the situation in the early Holocene, with large-amplitude variations between taxa and the progressive increase of typically light-dependent taxa such as *Ilex mitis*. Increased seasonality, combined with the gradual decrease of rainfall since the mid-Holocene noted above, may have been responsible for the progressive destabilization of forest, leading to its final collapse at 3.3 cal. kyr BP. Increased El Niño/Southern Oscillation (ENSO) (Clement *et al.*, 2000; Moy *et al.*, 2002) and sea surface temperature (SST) changes in the tropical Atlantic (Jury *et al.*, 2002), which have been suggested in relation to hydrological changes at Ossa (Nguetsop *et al.*, 2010), are possible mechanisms driving this climatic change (Fig. 6). Beyond the 3.3 cal. kyr BP tipping point, the Bambili montane forest was never able to fully recover. The retreat of the two main montane trees, *Podocarpus* and *Olea*, is not restricted to this specific area. Their pollen percentages strongly decrease from all the other pollen sites in Cameroon. This supports White's (1993) hypothesis that the montane forests are 'contemporary refuges'. Today, *Podocarpus latifolius* is present only on Mount Oku and Mount Kupé, while *Olea capensis* is also found on Mount Cameroon and the Adamawa plateau as relict populations (Letouzey, 1968, 1985).

The subsequent minor forest phases recorded at Bambili are characterized by a significant pollen presence of light-dependent trees, whereas the last 100 years are disproportionately lacking the diversity observed in earlier phases. The increase of *Olea* at 1 cal. kyr BP, unaccompanied by *Podocarpus*, reflects the dispersal ability of this pioneering taxon at the particular site of Bambili in a regional context of forest degradation. The fact that we do not find any trace of this minor *Olea* phase elsewhere in Cameroon suggests its local character.

CONCLUSIONS

The mountain forests of Cameroon are of recent origin and result from the idiosyncratic migration of trees from distinct sources. Post-glacial forest colonization at Bambili closely followed intensification of the Atlantic monsoon circulation after 18.4 cal. kyr BP in phase with orbitally controlled insolation forcing. Phases of more or less pronounced forest disturbance are coeval (within dating errors) with H1, the YD and the 8.2 ka event of the North Atlantic basin. This suggests teleconnections between monsoonal and high-latitude climate systems, involving both oceanic and atmospheric transmission linked to changes in the AMOC. Increased rainfall variability since the mid-Holocene, perhaps tied to more frequent ENSO events, is thought to have had long-term effects on ecosystem stability, which led to an irreversible

'tipping point' at 3.3 cal. kyr BP. Beyond this point, the forest was never able to fully recover. Floristic richness increased during phases of disturbance (the last glacial–interglacial transition and the end of the Holocene forest phase). During the last millennium, however, very severe disruptions meant that only the most dynamic species were able to spread (e.g. *Olea*). Forest disruptions are likely to have significantly contributed to the dramatic loss of forest biodiversity during the last millennium, a loss probably accentuated by human impact in the last few centuries.

REFERENCES

Alley, R.B. (2000) The Younger Dryas cold interval as viewed from central Greenland. *Quaternary Science Reviews*, **19**, 213–226.

Anthony, N.M., Johnson-Bawe, M., Jeffery, K., Clifford, S.L., Abernethy, K.A., Tutin, C.E., Lahm, S.A., White, L.J.T., Utley, J.F., Wickings, E.J. & Bruford, M.W. (2007) The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. *Proceedings of the National Academy of Sciences USA*, **104**, 20432–20436.

Asombang, R.N. (1998) Ten years of archaeological research in the Bamenda Grassfields. *Paléo-anthropologie en Afrique centrale: un bilan de l'archéologie au Cameroun* (ed. by M. Delneuf, J.M. Essomba and A. Froment), pp. 193–202. L'Harmattan, Paris.

Assi-Kaudjhis, C.C.-M. (2011) *Dynamique des écosystèmes et biodiversité des montagnes du Cameroun au cours des derniers 20 000 ans. Analyse palynologique d'une série sédimentaire du lac Bambili*. PhD Thesis, University of Liège, Belgium.

Assi-Kaudjhis, C., Digbehi, B.Z., Roche, E. & Lézine, A.-M. (2010) Synthèse sur l'évolution des paléoenvironnements de l'Afrique occidentale atlantique depuis la fin de la dernière période glaciaire. Influences climatiques et anthropiques. *Geo-Eco-Trop*, **34**, 1–28.

Bayon, G., Dennielou, B., Etoubleau, J., Ponzevera, E., Toucanne, S. & Bermel, S. (2012) Intensifying weathering and land-use in Iron Age Central Africa. *Science*, **335**, 1219–1222.

Beentje, H.J. (2002) Compositae (Part 2). *Flora of tropical East Africa* (ed. by H.J. Beentje and S.A.L. Smith), pp. 315–546. Balkema, Rotterdam.

Berger, A. & Loutre, M.-F. (1991) Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews*, **10**, 297–317.

Birks, H.J.B. & Line, J.M. (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene*, **2**, 1–10.

Bonnefille, R. & Riollet, G. (1988) The Kashiru pollen sequence (Burundi) palaeoclimatic implications for the last 40,000 yr BP in tropical Africa. *Quaternary Research*, **30**, 19–35.

Bonnefille, R., Riollet, G. & Buchet, G. (1991) Nouvelle séquence pollinique d'une tourbière de la crête Zaïre-Nil (Burundi). *Review of Palaeobotany and Palynology*, **67**, 315–330.

Bonnefille, R., Riollet, G., Buchet, G., Icole, M., Lafont, R., Arnold, M. & Jolly, D. (1995) Glacial/interglacial record from intertropical Africa, high resolution pollen and carbon data at Rusaka, Burundi. *Quaternary Science Reviews*, **14**, 917–936.

Boutrais, J. (1981) L'expansion des éleveurs peul dans les savanes humides du Cameroun. *Cahiers ORSTOM, Série Sciences Humaines*, **18**, 31–45.

Cheek, M. (2004a) *Schefflera mannii. IUCN Red List of Threatened Species. Version 2011.1*. Available at: http://www.iucnredlist.org (accessed 25 July 2012).

Cheek, M. (2004b) *Morella arborea. IUCN Red List of Threatened Species. Version 2011.1*. Available at: http://www.iucnredlist.org (accessed 25 July 2012).

Cheek, M., Onana, J.-M. & Pollard, B.J. (2000) *The plants of Mount Oku and the Ijim Ridge, Cameroon*. Royal Botanical Gardens, Kew.

Cheng, H., Fleitmann, D., Edwards, R.L., Wang, X., Cruz, F.W., Auler, A.S., Mangini, A., Yongjin, W., Xinggong, K., Burns, S.J. & Matter, A. (2009) Timing and structure of the 8.2 kyr B.P. event inferred from $\delta^{18}O$ records of stalagmites from China, Oman, and Brazil. *Geology*, **37**, 1007–1010.

Clement, A.C., Seager, R. & Cane, M.A. (2000) Suppression of El Niño during the mid-Holocene by changes in the Earth's orbit. *Paleoceanography*, **15**, 731–737.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptative response to Quaternary climate change. *Science*, **292**, 673–678.

Drake, J.M. & Griffen, B.D. (2010) Early warning signals of extinction in deteriorating environments. *Nature*, **467**, 456–459.

Elenga, H., Vincens, A. & Schwartz, D. (1991) Présence d'éléments forestiers montagnards sur les Plateaux Batéké (Congo) au Pléistocène supérieur: nouvelles données palynologiques. *Palaeoecology of Africa*, **22**, 239–252.

Faegri, K. & Iversen, J. (1975) *Textbook of pollen analysis.* Blackwell, Oxford.

Farrera, I., Harrison, S.P., Prentice, I.C., Ramstein, G., Guiot, J., Bartlein, P.J., Bonnefille, R., Bush, M., Cramer, W., von Grafenstein, U., Holmgren, K., Hooghiemstra, H., Hope, G., Jolly, D., Lauritzen, S.-E., Ono, Y., Pinot, S., Stute, M. & Yu, G. (1999) Tropical climates at the Last Glacial Maximum: a new synthesis of terrestrial palaeoclimate data. I. Vegetation, lake-levels and geochemistry. *Climate Dynamics*, **15**, 823–856.

Finch, J., Leng, M.J. & Marchant, R. (2009) Late Quaternary vegetation dynamics in a biodiversity hotspot, the Uluguru Mountains of Tanzania. *Quaternary Research*, **72**, 111–122.

Foster, P. (2001) The potential negative impact of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, **55**, 73–106.

Gasse, F. (2000) Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 189–211.

Gelorini, V. (2011) *Diversity and palaeoecological significance of non-pollen palynomorph assemblages in East African lake sediments.* PhD Thesis, University of Gent, Belgium.

von Grafenstein, U., Erlenkeuser, H., Müller, J., Jouzel, J. & Johnsen, S. (1997) The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. *Climate Dynamics*, **14**, 73–81.

Grimm, E.C. (1987) CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, **13**, 13–35.

Hamilton, A.C. (1982) *Environmental history of East Africa: a study of the Quaternary.* Academic Press, London.

Harvey, Y., Pollard, B.J., Darbyshire, I., Onana, J.-M. & Cheek, M. (2004) *The plants of Bali Ngemba Forest Reserve, Cameroon: a conservation checklist.* Royal Botanical Gardens, Kew.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Itambi, A.C., von Dobeneck, T. & Adegbie, A.T. (2010) Millennial-scale precipitation changes over Central Africa during the late Quaternary and Holocene: evidence in sediments from the Gulf of Guinea. *Journal of Quaternary Science*, **25**, 267–279.

Jolly, D. & Haxeltine, A. (1997) Effect of low glacial atmospheric CO_2 on tropical African montane vegetation. *Science*, **276**, 786–788.

Jolly, D., Bonnefille, R. & Roux, M. (1994) Numerical interpretation of a high resolution Holocene pollen record from Burundi. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **109**, 357–370.

Jowsey, P.C. (1966) An improved peat sampler. *New Phytologist*, **65**, 245–248.

Jury, M.R., Enfield, D.B. & Mélice, J.-L. (2002) Tropical monsoons around Africa: stability of El Niño–Southern Oscillation associations and links with continental climate. *Journal of Geophysical Research*, **107** (C10), 3151.

Kadomura, H. & Kiyonaga, J. (1994) Origin of grassfields landscape in the West Cameroon Highlands. *Savannization processes in tropical Africa II* (ed. by H. Kadomura), pp. 47–85. Tokyo Metropolitan University, Japan.

Kadu, C.A.C., Schueler, S., Konrad, H., Muluvi, G.M.M., Eyog-Maig, O., Muchugi, A., Williams, V.L., Ramamonjisoa, L., Kapinga, C., Foahom, B., Katsvanga, C., Hafashimana, D., Obama, C. & Geburek, T. (2011) Phylogeography of the Afromontane *Prunus africana* reveals a former migration corridor between East and West African highlands. *Molecular Ecology*, **20**, 165–178.

Kim, S.-Y., Scourse, J., Marret, F. & Lim, D.-I. (2010) A 26,000-year integrated record of marine and terrestrial environmental change off Gabon, west equatorial Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **297**, 428–438.

Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.-P., Fagot, M., Rumes, B., Russell, J.M., Darius, F., Conley, D.J., Schuster, M., von Suchodoletz, H. & Engstrom, D.R. (2008) Climate-driven ecosystem succession in the Sahara: the past 6000 years. *Science*, **320**, 765–768.

Lebamba, J., Vincens, A. & Maley, J. (2012) Pollen, vegetation change and climate at Lake Barombi Mbo (Cameroon) during the last ca. 33 000 cal yr BP: a numerical approach. *Climate of the Past*, **8**, 59–78.

Lebrun, J. & Gilbert, G. (1954) *Une classification écologique des forêts du Congo.* INEAC, Série Scientifique No. 63, Bruxelles.

Letouzey, R. (1968) *Étude phytogéographique du Cameroun.* Lechevalier, Paris.

Letouzey, R. (1985) *Notice de la carte phytogéographique du Cameroun au 1 : 500 000.* Institut de la Carte Internationale de la Végétation, Toulouse, France.

Lézine, A.-M. (1988) Les variations de la couverture forestière mésophile d'Afrique occidentale au cours de l'Holocène. *Comptes Rendus de l'Académie des Sciences, Paris*, **307**, 439–445.

Lézine, A.-M. (1989) Late Quaternary vegetation and climate of the Sahel. *Quaternary Research*, **32**, 317–334.

Lézine, A.-M. (2007) Postglacial pollen records of Africa. *Encyclopaedia of Quaternary Science*, Vol. 4 (ed. by S.A. Elias), pp. 2682–2698. Elsevier, Amsterdam.

Lézine, A.-M. & Vergnaud-Grazzini, C. (1993) Evidence of forest extension in West Africa since 22,000 BP: a pollen record from the eastern Tropical Atlantic. *Quaternary Science Reviews*, **12**, 203–210.

Lézine, A.-M., Duplessy, J.-C. & Cazet, J.-P. (2005) West African monsoon variability during the last deglaciation and the Holocene: evidence from fresh water algae, pollen and isotope data from core KW31, Gulf of Guinea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **219**, 225–237.

Lézine, A.-M., Hély, C., Grenier, C., Braconnot, P. & Krinner, G. (2011) Sahara and Sahel vulnerability to climate changes, lessons from paleohydrological data. *Quaternary Science Reviews*, **30**, 3001–3012.

Livingstone, D.A. (1967) Postglacial vegetation of the Ruwenzori Mountains in equatorial Africa. *Ecological Monographs*, **37**, 25–52.

Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.

Lovett, J.C. (1993) Eastern Arc moist forest flora. *Biogeography and ecology of the rainforests of Eastern Africa* (ed. by J.C. Lovett and S.K. Wasser), pp. 33–55. Cambridge University Press, Cambridge, UK.

Lovett, J.C. (1996) Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology*, **12**, 629–650.

Lovett, J.C. (1999) Tanzanian forest tree plot diversity and elevation. *Journal of Tropical Ecology*, **15**, 689–694.

Maley, J. & Brenac, P. (1998) Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Review of Palaeobotany and Palynology*, **99**, 157–187.

Marchant, R. & Hooghiemstra, H. (2004) Rapid environmental change in African and South American tropics around 4000 years before present: a review. *Earth-Science Reviews*, **66**, 217–260.

Marzin, C. & Braconnot, P. (2009) Variations of Indian and African monsoons induced by insolation changes at 6 and 9.5 kyr BP. *Climate Dynamics*, **33**, 215–231.

deMenocal, P.B., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L. & Yarusinski, M. (2000) Abrupt onset and termination of the African Humid Period: rapid climate response to gradual insolation forcing. *Quaternary Science Reviews*, **19**, 347–361.

Momo Solefack, M.C. (2009) *Influence des activités anthropiques sur la végétation du Mont Oku (Cameroun)*. PhD Thesis, Université de Picardie, Amiens, France.

Moy, C.M., Seltzer, G.O., Rodbell, D.T. & Anderson, D.M. (2002) Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature*, **420**, 162–165.

Mumbi, C.T., Marchant, R., Hooghiemstra, H. & Wooller, M.J. (2008) Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania. *Quaternary Research*, **69**, 326–341.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Ngomanda, A., Neumann, K., Schweizer, A. & Maley, J. (2009) Seasonality change and the third millennium BP rainforest crisis in southern Cameroon (Central Africa). *Quaternary Research*, **71**, 307–318.

Nguetsop, V.F., Servant-Vildary, S., Servant, M. & Roux, M. (2010) Long and short-time scale climatic variability in the last 5500 years in Africa according to modern and fossil diatoms from Lake Ossa (Western Cameroon). *Global and Planetary Change*, **72**, 356–367.

North Greenland Ice Core Project members (2004) High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature*, **431**, 147–151.

Peros, M.C. & Gajewski, K. (2008) Testing the reliability of pollen-based diversity estimates. *Journal of Paleolimnology*, **40**, 357–368.

Reimer, P.J., Baillie, M.G.L., Bard, E. *et al.* (2004) IntCal04 terrestrial radiocarbon age calibration, 0–26 cal kyr BP. *Radiocarbon*, **46**, 1029–1058.

Reynaud-Farrera, I., Maley, J. & Wirrmann, D. (1996) Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4770 ans BP: analyse pollinique des sédiments du Lac Ossa. *Comptes Rendus de l'Académie des Sciences, Paris*, **322**, II a, 749–755.

Richards, K. (1986) Preliminary results of pollen analysis of a 8,000 years core from Mboandong, a crater lake in Cameroon. *The Hull University Cameroon Expedition 1981–1982* (ed. by K. Baker, K. Richards and C.A. Rimes), pp. 14–28. Department of Geography, University of Hull, UK.

Runge, J. (2002) Holocene landscape history and palaeohydrology evidenced by stable carbon isotope (δ^{13}C) analysis of alluvial sediments in the Mbari valley (5°N/23°E), Central African Republic. *Catena*, **48**, 67–87.

Salzmann, U. & Hoelzmann, P. (2005) The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene*, **15**, 190–199.

Salzmann, U. & Waller, M. (1998) The Holocene vegetational history of the Nigerian Sahel based on multiple pollen profiles. *Review of Palaeobotany and Palynology*, **100**, 39–72.

Salzmann, U., Hoelzmann, P. & Morczinek, I. (2002) Late Quaternary climate and vegetation of the Sudanian zone of northeast Nigeria. *Quaternary Research*, **58**, 73–83.

Sangen, M., Neumann, K. & Eisenberg, J. (2011) Climate-induced fluvial dynamics in tropical Africa around the last glacial maximum? *Quaternary Research*, **73**, 417–429.

Sarnthein, M., Tetzlaff, G., Koopman, B., Wolter, K. & Pflaumann, U. (1981) Glacial and interglacial wind regimes over the eastern subtropical Atlantic and north-west Africa. *Nature*, **293**, 193–196.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Shanahan, T.M., Overpeck, J.T., Wheeler, C.W., Beck, J.W., Pigati, J.S., Talbot, M.R., Scholz, C.A., Peck, J. & King, J.W. (2006) Paleoclimatic variations in West Africa from a record of late Pleistocene and Holocene lake level stands of Lake Bosumtwi, Ghana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **242**, 287–302.

Smith, B. & Wilson, J.B. (1996) A consumer's guide to evenness indices. *Oikos*, **76**, 70–82.

Stager, J.C. & Anfang-Sutter, R. (1999) Preliminary evidence of environmental changes at Lake Bambili (Cameroon, West Africa) since 24,000 BP. *Journal of Paleolimnology*, **22**, 319–330.

Stager, J.C., Majewski, P.A. & Meeker, L.D. (2002) Cooling cycles, Heinrich event 1, and the desiccation of Lake Victoria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183**, 169–178.

Stanford, J.D., Rohling, E.J., Bacon, S., Roberts, A.P., Grousset, F.E. & Bolshaw, M. (2011) A new concept for the paleoceanographic evolution of Heinrich event 1 in the North Atlantic. *Quaternary Science Reviews*, **30**, 1047–1066.

Stuiver, M. & Reimer, P.J. (1993) Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. *Radiocarbon*, **35**, 215–230.

Suchel, J.B. (1988) *Les climats du Cameroun*. PhD Thesis, University of Saint-Etienne, France.

Talbot, M.R., Livingstone, D.A., Palmer, P.G., Maley, J., Melack, J.M., Delibrias, G. & Gulliksen, S. (1984) Preliminary results from sediment cores from Lake Bosumtwi, Ghana. *Palaeoecology of Africa*, **16**, 173–192.

Tamura, T. (1990) Late Quaternary landscape evolution in the West Cameroon Highlands and the Adamaoua Plateau. *Paysages quaternaires de l'Afrique centrale atlantique* (ed. by R. Lanfranchi and D. Schwartz), pp. 298–318. ORSTOM, Paris.

Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C. & Woodward, F.I. (2006) Endemic species and ecosystem sensibility to climate change in Namibia. *Global Change Biology*, **12**, 759–776.

Vincens, A., Casanova, J. & Tiercelin, J.J. (1986) Palaeolimnology of Lake Bogoria (Kenya) during the 4500 BP high lacustrine phase. *Sedimentation in the African Rifts* (ed. by L.E. Frostick, R.W. Renaut, I. Reid and J.J. Tiercelin), pp. 323–330. Geological Society Special Publication No. 25, London. Blackwell Scientific Publications, Oxford.

Vincens, A., Schwartz, D., Bertaux, J., Elenga, H. & de Namur, C. (1998) Late Holocene climatic changes in western equatorial Africa inferred from pollen from Lake Sinnda, southern Congo. *Quaternary Research*, **50**, 34–45.

Vincens, A., Schwartz, D., Elenga, H., Reynaud-Farrera, I., Alexandre, A., Bertaux, J., Mariotti, A., Martin, L., Meunier, J.-D., Nguetsop, F., Servant, M., Servant-Vildary, S. & Wirrmann, D. (1999) Forest response to climate change in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *Journal of Biogeography*, **26**, 879–885.

Vincens, A., Buchet, G., Servant, M. & ECOFIT Mbalang collaborators (2010) Vegetation response to the "African Humid Period" termination in Central Cameroon (7° N) – new pollen insight from Lake Mbalang. *Climate of the Past*, **6**, 281–294.

Watrin, J., Lézine, A.-M., Gajewski, K. & Vincens, A. (2007) Pollen–plant–climate relationships in sub-Saharan Africa. *Journal of Biogeography*, **34**, 489–499.

Watrin, J., Lézine, A.-M. & Hély, C. (2009) Plant migration and plant communities at the time of the "green Sahara". *Comptes Rendus Geosciences*, **341**, 656–670.

Weldeab, S., Lea, D.W., Schneider, R.R. & Andersen, N. (2007) 155,000 years of West African monsoon and ocean thermal evolution. *Science*, **316**, 1303–1307.

White, F. (1983) *The vegetation of Africa*. UNESCO, Paris.

White, F. (1993) Refuge theory, ice-age aridity and the history of tropical biotas: an essay in plant geography. *Fragmenta Floristica et Geobotanica*, Supplement 2, 385–409.

Williams, J.W., Blois, J.L. & Shuman, B.N. (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology*, **99**, 664–677.

Wooler, M.J., Swain, D.L., Ficken, K.J., Agnew, A.D.Q., Street-Perrott, F.A. & Eglinton, G. (2003) Late Quaternary vegetation changes around Lake Rutundu, Mount Kenya, East Africa: evidence from grass cuticles, pollen and stable carbon isotopes. *Journal of Quaternary Science*, **19**, 703–711.

Wu, H., Guiot, J., Brewer, S., Guo, Z. & Peng, C. (2007) Dominant factors controlling glacial and interglacial variations in the treeline elevation in tropical Africa. *Proceedings of the National Academy of Sciences USA*, **104**, 9720–9724.

SUPPORTING INFORMATION

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

Appendix S1 Depth–age model of the Bambili sequence, western Cameroon.
Appendix S2 Pollen identification.

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BIOSKETCH

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Author contributions: A.-M.L. initiated and coordinated the research, carried out statistical analyses and wrote the paper; C.A.K. provided the data set; G.A. interpreted the ecological/botanical data; and A.V. and E.R. used their expertise in tropical palynology to improve the data set and the manuscript.

Editor: Jack Williams