PALEOECOLOGY

A 90,000-year record of Afromontane forest responses to climate change

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Pollen records from African highlands are scarce; hence, the paleoecology of the Afromontane forest and its responses to glacial cycles are poorly known. Lake Bambili (Cameroon) provides a record of vegetation changes in the tropical mountains of Africa over the past 90,000 years, with high temporal resolution. Pollen data and biome reconstructions show a diverging response of forests to climate changes; the upper tree line was extremely unstable, shifting substantially in response to glacial-interglacial climate alternation, whereas the transition between the montane and lowland forests remained remarkably stable. Such ecological instability may have had a critical influence on species richness in the Afromontane forests.

Whether stability or instability of tropical forests has produced their high biodiversity has long been debated. The high endemism and/or species richness in the rain forest of Equatorial Africa has been attributed to contraction to isolated blocks or refugia during unfavorable climates, such as those of the glacial periods of the Quaternary. It has been postulated that forest remnants persisted in refugia within a grassland-dominated landscape (*1*), with the long-term ecological stability in these restricted areas promoting high levels of species richness and endemism. Both pollen and genetic data have been invoked in support this "glacial refuge theory." Pollen records of the last glacial period mainly comes from marine cores that give information on large-scale environmental change that includes multiple vegetation zones across a large region and thus cannot be used to trace variation in plant community biodiversity locally (*2*). Continental records are scarce and located at the edge of the rain forest. The story they deliver is therefore particularly heterogeneous, with evidence for ecological stability at Ngamakala, Congo, to the south of the rain forest (*3*), contrasting with severe forest contractions at Lake Barombi Mbo, Cameroon (*4*, *5*), and Lake Bosumtwi, Ghana (*6*, *7*), to the north. Genetic data confirm that the lowland forests likely experienced multiple phases of contraction and expansion, of which the precise location and chronology remain unresolved (*8*).

Unlike the lowland areas, equatorial mountains are thought to have provided a stable moist habitat throughout the glacial episodes (*9*), allowing persistence of biodiversity-rich montane forests to the present day. Alternatively, White (*10*) hypothesized that Afromontane forest communities reached their current distribution in the highlands of western Equatorial Africa only during the Holocene and as such can be considered as "contemporary refugia." Here, we present a 90,000-year-long pollen sequence of Afromontane vegetation from Lake Bambili, a high-altitude crater lake in Cameroon (05° 56′ 11.9 N, 10°14′ 31.6 E, 2273 m above sea level) (Fig. 1) that reveals the stability and instability of equatorial Afromontane biomes through time as a driver of biological richness in one of the principal centers of biodiversity in Africa (*11*).

Lake Bambili is formed by two adjacent crater basins (Fig. 1) in the center part of the Cameroon Volcanic Line, which culminates at Mt. Oku (3011 m). The upper crater is a marsh, whereas the lower crater, situated less than 100 m below, is filled by a shallow lake (4 to 6 m deep) and receives overflow from the upper crater. Bambili is situated in the Afromontane forest belt, which currently lies ~1800 to 2800 m above sea level and is characterized by the presence of *Podocarpus milanjianus*, the only conifer indigenous to Cameroon. This forest is bounded at the top by Afroalpine grasslands and at the bottom by submontane forests and savannas, forming the transition with rain forests and seasonal forests of the Guineo-Congolian phytogeographic zone (fig. S1) (*12*). Bambili lies under the influence of the African monsoon system (Fig. 1). The average of annual precipitation is 2000 mm, with a maximum in July through September. Rains are intense and regularly distributed with 5 months above 200 mm, and mists are frequent during the rainy seasons. At the altitude of Bambili, mean monthly temperature does not exceed 18°C, and frost is very rare (*13*).

The Bambili composite record consists of two coring sections recovered at the lower crater lakeshore (B1) and inside the upper crater (B2), respectively (*14*). The sediment is uniformly organic, with less decomposed organic matter in the uppermost meters of B1. Core B1 (14 m long) has yielded a continuous pollen sequence from 20 thousand years (ka) ago to the present, described in detail elsewhere (*15*, *16*). The time scale of core B2 (12.60 m long) was constrained

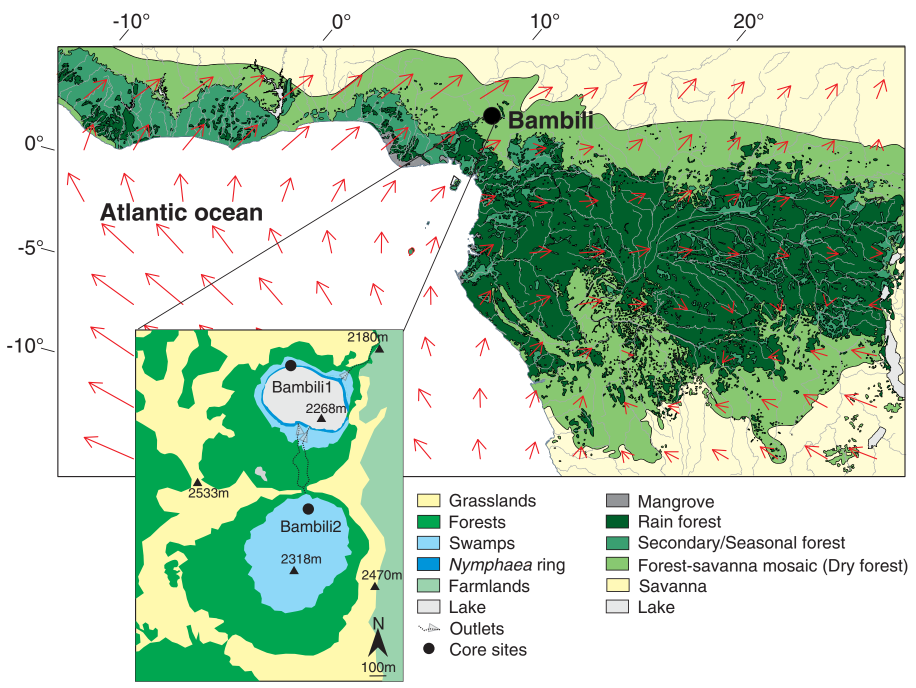

Fig. 1. Location of Bambili in western Equatorial Africa. The map shows the main vegetation types (*10*). Red arrows indicate the strength and direction of the main 925 hPa monsoonal winds during summer (NCEP-DOE AMIP-II Reanalysis). (**Inset**) The location of the core sites in the Bambili twin crater system, with details of local vegetation distribution.

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by fitting a third-order polynomial curve to the profile of 12 AMS radiocarbon dates against depth (tables S1 and S2). In the absence of tephra horizons, we used correlation with past phases of expanded tree cover registered in the adjacent marine pollen record from site GIK 16856-2 offshore Cameroon (*2*) to confirm the radiocarbon chronology of B2 while giving additional control points for the base of the sequence. The resulting chronology shows that core B2 represents a continuous record down to the base of the sequence, dated at 88.9 ka ago. The filling of the upper crater basin was fully completed during the early Holocene. Because the uppermost 1.54 m of B2 overlap in time with B1, they were not used. The accuracy of the B2 chronology depends on whether the pollen record of past forest expansion and contraction in marine core GIK-15856-2 is representative of the large-scale environment on the adjacent continent, including the montane forests of NW Cameroon. The Bambili chronology that resulted from peak matching of total tree percentages (excluding mangrove) at both sites is coherent and also fits with the ^{14}C-dated portion of the Bambili sequence.

The relative abundance of woody taxa (trees and shrubs pollen percentages) allows distinction of three forest phases (Figs. 2 and 3, B and D), separated by episodes of grassland development. Expansion of forests at Bambili was closely coeval with the wide development of lakes and vegetation cover and the resulting weakening of dust fluxes from the desert (fig. S2). All these testify for moist conditions over northern Africa linked to enhanced monsoon rainfall (supplementary text). Major forest phases occurred from 82.6 to 72 ka ago during the Last Interglacial (MIS 5) and from 10 to 3.3 ka ago during the Holocene. These forest phases strongly differed from each other, in that the Holocene phase consisted of two forest biomes (tables S3 to S5) (*14*), the lower-level montane forest (WAMF) and the lowland tropical seasonal forest (TSFO), whereas the MIS 5 forest phase included WAMF and upper-level Afromontane forest (AAF), which show the upper tree limit. A third phase of more moderate forest development occurred from 53 to 38 ka ago during MIS 3. As during MIS 5, this interval was characterized by WAMF and AAF, but the lower proportion of woody taxa compared with the other two forest phases, and the coeval importance of Afro-alpine grassland (AAG) and low/mid-elevation savanna (SAVA) biomes, indicates that the mountain-forest zone during MIS 3 had a relatively narrow altitudinal range.

Grass-dominated biomes were consistently present at Bambili throughout the glacial periods. Savannas occurred continuously outside the intervals of forest expansion. Afro-alpine grasslands dominated from 72 to 15.5 ka ago (from MIS 4 to MIS 2) and during a short interval at the MIS 5 ~82 ka ago. Lowland steppe (STEP) and desert (DESE) biomes occurred during the glacial maxima, particularly MIS 2. Together with the near-absence of forest elements (Fig. 2), this makes the last glacial period (MIS 2) undoubtedly the driest episode over the past 90 ka in western Equatorial Africa. By contrast, the penultimate glacial period (MIS 4) was characterized by the noticeable occurrence of subalpine trees and shrubs (such as Ericaceae), showing that the montane forests remained present in the Bambili area at that time as extremely degraded formations dominated by upper treeline elements.

In East Africa, the expansion of mountain glaciers during the last glacial period (*17*) was accompanied by a downward displacement of the upper treeline, such as subalpine taxa growing down to the surroundings of Lake Tanganyika at 773 m above sea level (*18*, *19*). Unlike East Africa, there is no evidence of past glacier formations in the highlands of western Equatorial Africa. However, continental and marine pollen data (*2*, *3*) suggest that Afromontane trees were more widely distributed during the last glacial period than today at the equator and southward (*2*). Although several living trees of *P. milanjianus* currently occur down to 900 m above sea level in Cameroon outside Mount Oku, as probable relicts of a formerly wider distribution, there is no direct evidence that this expansion took place during MIS 2: *P. milanjianus* was absent at that time from Lake Barombi Mbo (600 m above sea level) (*4*) and Lake Monoun (1083 m above sea level). It was only found in a single pollen sample dated 28,700 ± 1800 ^{14}C BP at Shum Laka at 1369 m above sea level (within the current elevation range of the species) (*20*). Another Afromontane tree, *Olea capensis*, has been extremely dynamic and able to migrate to low altitudes during the Last Glacial Maximum

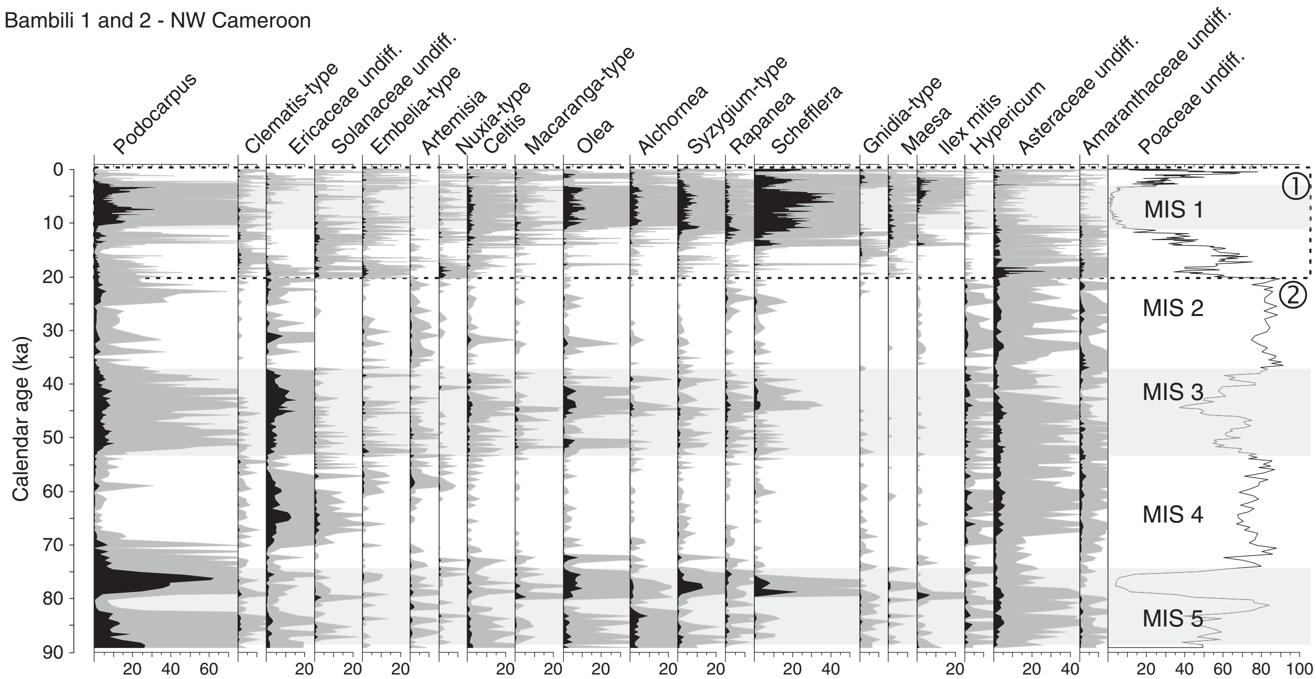

Fig. 2. Percentage pollen diagram of selected taxa from Bambili. Black shading indicates selected taxa versus time. Gray shading shows the same results, multiplied by 10 for highlighting. Percentages are calculated against the sum of terrestrial plants, excluding aquatics. The pollen analysis comprised 385 samples and 275 identified pollen and fern-spore types. Gray bands indicate the forest phases.

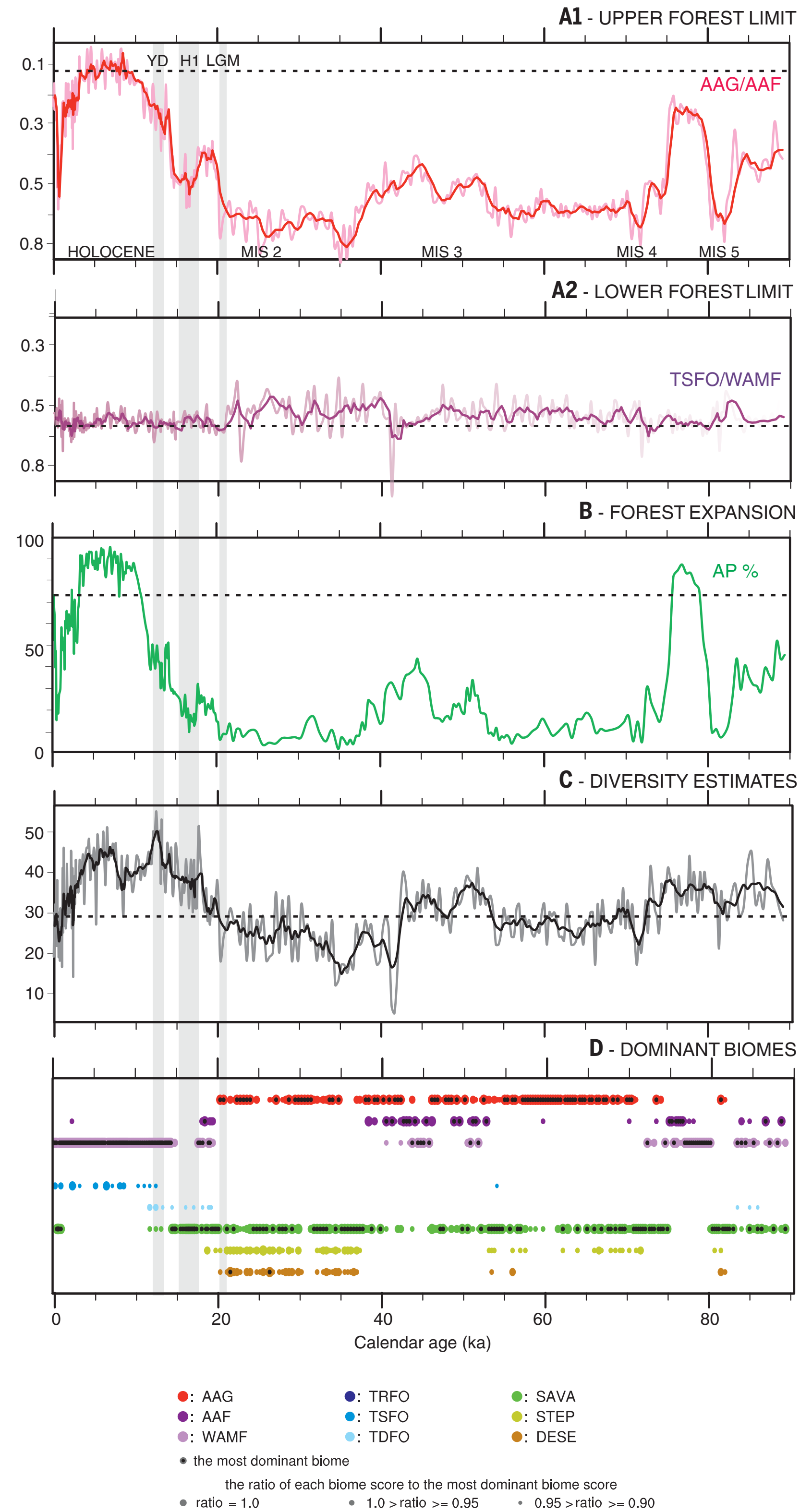

Fig. 3. Evolution of equatorial montane forests of western Africa over the past 90 ka based on Lake Bambili pollen record. (**A1** and **A2**) AAG/AAF and TSFO/WAMF biome ratios, respectively. (**B**) Tree pollen percentages. (**C**) Diversity estimates from rarefaction analyses on terrestrial pollen data. (**D**) Dominant biomes reconstruction (*14*) (tables S3-5). Horizontal dotted lines in (A), (B), and (C) show the modern-day levels. Bold lines in (A) and (C) represent the five-sample running means. Gray vertical bands show the Younger Dryas (YD); Heinrich 1 (H1) events and the Last Glacial Maximum (LGM). Biome definitions are provided in table S4.

(LGM) and then to recolonize mountain areas during the postglacial warming (*14*). However, we cannot deduce the treeline migration of Afromontane forest as a whole from the individual species behavior. To investigate the amplitude of the treeline migration and expansion/contraction of Afromontane forest range, we define the upper and lower Afromontane forest limits as follows: The upper limit is defined by the AAG/AAF ratio, and the lower limit is defined by the TSFO/WAMF ratio. Even though shifts of the upper treeline cannot be precisely quantified from the present study, evidence for the considerable amplitude of these shifts is unequivocal. Three main features arise from the AAG/AAF ratio (Fig. 3A1): (i) The upper treeline was displaced upward with respect to its current average position only during the early to mid-Holocene portion of the African Humid Period (*21*). This upslope expansion was necessarily limited because of the proximity of the summit. (ii) The upper tree line reached its lowermost elevation around 35 ka ago. Its subsequent upslope expansion started well before the LGM but accelerated immediately after it (~20 ka ago). The expansion paused and even reversed close to its LGM position during the Heinrich 1 severe drought (*22*). The upslope movement resumed at ~15 ka ago to reach the modern-day treeline elevation by the onset of the Holocene (11 ka ago). (iii) The major upslope/downslope movements of the upper tree line often occurred within a few centuries (or even a few decades), testifying to the sensitivity of the Afromontane ecosystems to change in environmental conditions. In comparison, the lower limit of the Afromontane forest displays remarkable stability around its present-day level throughout the past 90 ka (Fig. 3A2). TSFO/WAMF increased only slightly during the glacial periods and mostly during MIS 2, suggesting a moderate upward development of lowland forests at the expense of the Afromontane ones.

The most remarkable result of our study is the ecological instability of the Afromontane forest belts compared with the relative stability of lowland tropical seasonal forest over the past 90 ka. It is at its upper limit that the Afromontane forest was the most vulnerable to changing climate. By contrast, the lower limit remained relatively stable, an observation that challenges the traditional paradigm of the equatorial forest block becoming fragmented during the last glacial period (*1*). Moreover, it confirms model simulations of paleoclimate and biome distribution that point to the continuous presence of equatorial forests in Africa during the LGM (*23*). Despite the instability at the upper limit, our results show that Afromontane forest biomes have persisted over the past 90 ka, albeit at varying extent, suggesting somewhat buffered environmental conditions in the Cameroon highlands.

Unlike Afromontane forest in the Eastern Arc Mountains of Tanzania, where high modern-day biodiversity is thought to have resulted from the remarkable long-term ecological stability observed during the past 40 ka (*24*), the diversity of vegetation in Cameroon Highlands was highly variable through time (Fig. 3C), which is consistent with the observed ecological instability (Fig. 3, A1 and B). Minimum values of diversity were coeval with the lowest position of the upper treeline between ~35 and 26 ka ago, whereas higher values than present-day pollen richness were reached during phases of forest expansion. The survival of residual forest populations in sheltered habitats within the Afromontane forest belt (such as Shum Laka) during the glacial period may have contributed to high species turnover during the last glacial-interglacial transition. The increase in diversity estimates started well before the LGM and accelerated from 20 ka ago onward. The highest diversity was then reached during the Younger Dryas dry event (~12.9 to 11.7 ka ago) (*25*), during a phase of major ecological disturbance and not during the following early Holocene phase of forest stability at 10 to 9 ka ago (*15*).

The Lake Bambili record shows that Afromontane forests of Cameroon are neither "glacial" nor "contemporary" refugia. Glacial climates did not lead to forest disappearance but had a major impact on the upper treeline, which shifted dramatically, revealing the sensitivity of the upper montane biomes to climate change.

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ACKNOWLEDGMENTS

Thanks are due to the Institut de Recherche pour le Développement (IRD), the Ministry of Research, and the National Herbarium in Cameroon for research facilities and authorizations; to G. Buchet, J.-P. Cazet, L. Février, and K. Lemonnier (CNRS) for laboratory and field assistance; and to D. Verschuren (Gent University, Belgium) and R. Cheddadi (CNRS Montpellier, France) for comments on earlier versions of the text. **Funding:** This research was supported by the National Research Agency (ANR), France, through IFORA (ANR-06-BDIV-0014), C3A (ANR-09-PEXT-001), VULPES (ANR-15-MASC-0003), and the BR/132/A1/AFRIFORD project in Belgium. K.I. was funded by a Marie Sklodowska-Curie European Individual Fellowship (H2020-MSCA-IF-EF, 705895), and A.-M.L. and M.K. were funded by CNRS. **Author contributions:** A.-M.L. designed the study. K.I. produced biome reconstructions. G.A. coordinated the research in the field. A.-M.L. prepared manuscript. All the authors analyzed the data and reviewed the manuscript. **Authors competing interests:** Authors have no competing interests. **Data availability:** Data are available from the NEOTOMA paleoecology database (www.neotomadb.org) and directly from the first author.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6423/177/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 and S2
Tables S1 to S5
References (*26*–*47*)

10 October 2018; accepted 6 December 2018
10.1126/science.aav6821

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Science **363** (6423), 177-181.
DOI: 10.1126/science.aav6821

Ancient changes in the African tropics

Long-term records of past vegetation change are key to understanding how climate change affects ecosystems, but data are scarce––especially in highly biodiverse regions in the tropics. Lezine *et al.* present a detailed 90,000-year pollen core from an upland crater-lake site in the west African tropical montane forest, which is important from conservation and biogeographic standpoints. The upper treeline moved in response to climate change during the Pleistocene glacial and interglacial periods, whereas the lower limit of the Afromontane forest was stable. The constituent species of the forest also changed. This record resolves debates concerning the biogeographic history of Afromontane vegetation.

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