

Forest extent and deforestation in tropical Africa since 1900

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Accurate estimates of historical forest extent and associated deforestation rates are crucial for quantifying tropical carbon cycles and formulating conservation policy. In Africa, data-driven estimates of historical closed-canopy forest extent and deforestation at the continental scale are lacking, and existing modelled estimates diverge substantially. Here, we synthesize available palaeo-proxies and historical maps to reconstruct forest extent in tropical Africa around 1900, when European colonization accelerated markedly, and compare these historical estimates with modern forest extent to estimate deforestation. We find that forests were less extensive in 1900 than bioclimatic models predict. Resultantly, across tropical Africa, ~21.7% of forests have been deforested, yielding substantially slower deforestation than previous estimates (35–55%). However, deforestation was heterogeneous: West and East African forests have undergone almost complete decline (~83.3 and 93.0%, respectively), while Central African forests have expanded at the expense of savannahs (~1.4% net forest expansion, with ~135,270 km² of savannahs encroached). These results suggest that climate alone does not determine savannah and forest distributions and that many savannahs hitherto considered to be degraded forests are instead relatively old. These data-driven reconstructions of historical biome distributions will inform tropical carbon cycle estimates, carbon mitigation initiatives and conservation planning in both forest and savannah systems.

Deforestation from tropical land-use change is a major global contributor to anthropogenic carbon emissions¹, changes in carbon and water cycles² and biodiversity loss³. Although tropical forests are not of exclusive interest, they are exceptionally diverse³ and represent one of the largest terrestrial carbon sinks⁴, making them an outsized component of the global carbon budget with major feedbacks on the climate system⁵. Thus, estimating land-use impacts on the climate system and biosphere relies directly on accurate estimates of historical forest extent and deforestation rates in the tropics. In South America and Southeast Asia, these are relatively well-constrained based on data^{6,7}. However, in Africa, a paucity of continental-scale data has led to divergent forest extent and deforestation estimates^{8,9}. The most widely cited estimates suggest radically high deforestation rates: between 35 and 55% of tropical forest in Africa deforested since AD 1900 (refs ^{10,11}), including more than 90% of West African^{7,12} and 74–100% of East African forests¹³ (Table 1).

The most widely cited assessments of pan-African historical forest extent¹⁴ and deforestation⁷ have been based on ‘potential natural vegetation’ modelled solely with modern bioclimatic variables¹⁵, rather than empirical observations of forest extent. This is problematic, since a growing body of evidence suggests that climate alone does not determine biome distributions, especially where vegetation–environment feedbacks are significant¹⁶. Tropical savannahs are a prime example; positive feedbacks between an open tree canopy and fire may substantially expand savannah beyond its climatically prescribed range. Today, ~36% of African savannahs currently occur where rainfall is sufficient for forest canopy closure¹⁶ and at least some of these may have persisted for millennia¹⁷. As a direct result of the non-deterministic relationship between biome and climate, models based solely on bioclimatic conditions^{14,15} may have substantially over-estimated historical forest extent and, thus, deforestation^{8,9}.

Over-estimating deforestation has direct consequences for land-use and conservation planning in the tropics¹⁸. Large areas of tropical

savannah may have been misidentified as being of recent anthropogenic origin and consequently targeted for reforestation in carbon mitigation initiatives¹⁹ and for biofuel production²⁰. By treating savannahs as suitable for agricultural conversion or afforestation^{21,22}, these studies implicitly assume mesic savannah biodiversity and function to be less deserving of conservation than forests. In reality, savannahs support a range of key ecosystem services, including plant and animal biodiversity and key biogeochemical and hydrological processes, as well as providing a critical source of livelihoods as cattle rangelands^{18,23}. Improved estimates of African historical forest extent and deforestation rates will be essential for avoiding misdirected restoration efforts.

Here, we synthesize available empirical data to statistically model forest extent across x at the beginning of the twentieth century (hereafter, ‘historical forest extent’) and to produce improved estimates of deforestation since this period. We chose AD 1900 as the baseline^{14,15} for reconstruction as the best compromise between minimal colonial impacts on the environment and data availability, since both historical maps and data from palaeoecological sites dating from AD 1900 exist. The year AD 1900 corresponds to the beginning of widespread European colonization^{24,25}; while Europeans were active in Africa long before 1900 and some of their impacts certainly predate 1900, active land-use change started to accelerate colonial impacts on forest and savannah areas around this time^{24,26}.

To do this, we assembled information about past vegetation from palaeo-proxies—pollen, phytoliths, stable carbon isotopes ($\delta^{13}\text{C}$) and charred macro-remains recovered from lake sediments and soil profiles (see Methods; Fig. 1). We included a total of 180 samples from palaeo sites (Supplementary Data 1), most of which were from Central, Eastern and Southern tropical Africa (Fig. 1). The available palaeo sites did not provide complete coverage over all of tropical Africa, especially West Africa and the Democratic Republic of Congo and, as such, were insufficient to accurately

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Table 1 | Comparison of estimated historical forest extent (around AD 1900) and associated deforestation rates (AD 1900–2000) with previously published estimates

Area	Previous estimates		This study	
	Historical forest extent (km ²)	Deforestation (%)	Historical forest extent (km ²)	Deforestation (%)
West Africa				
Benin, Ghana, Guinea, Côte d'Ivoire, Liberia, Sierra Leone and Togo	762,700 ¹²	−90.3 ^a	424,842	−82.5
Benin, Ghana, Côte d'Ivoire, Liberia, Sierra Leone and Togo	105,000 to 486,000 ³²	−29.5 to −84.8 ^a	391,618	−81.1
Benin, Ghana, Côte d'Ivoire and Liberia	319,660 ⁴⁹	−78.1 ^a	339,272	−79.4
East Africa				
Eastern Arc Mountain	NA	−74 ¹³	85,087	−100
Ethiopia	420,000 ⁵⁰	−92.5 ⁵⁰ , −100 ^a	60,940	−100
Uganda	NA	−92.5 ⁵¹	51,290	−92.3
Central Africa				
NA	−47.8 ³³	2,033,920	+1.4	
Tropical Africa (total)				
NA	−35 ¹¹ , −39.6 ³³ , −55 ^{10,31}	3,527,307	−21.7	

^aDeforestation rate computed using published historical forest extent and modern (AD 2000) forest extent estimates from this study. NA, not available.

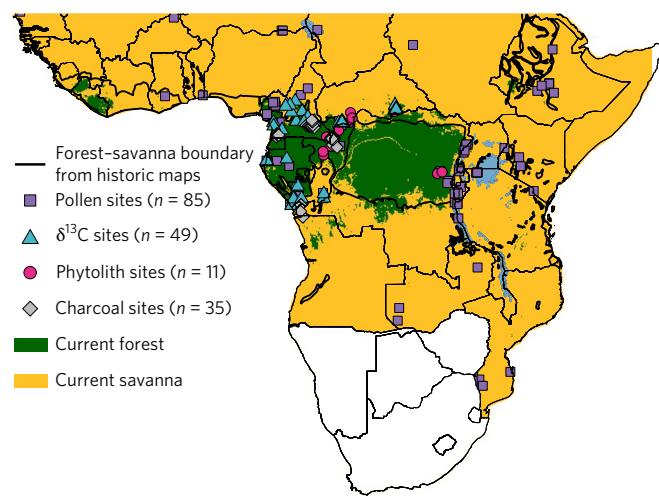


Fig. 1 | Palaeo-proxy sites and locations of historical maps used as inputs for modelling the forest extent in the year AD 1900. Palaeo-data sources are overlaid on a map of modern tree cover distributions from ref. ²⁷, with a tree cover threshold of 70% to differentiate savannah from forest (see Supplementary Fig. 2). Source : Hansen/UMD/Google/USGS/NASA; data available on-line from: <http://earthenginepartners.appspot.com/science-2013-global-forest>.

reconstruct forest extent. We therefore supplemented palaeo-data with the available historical forest maps in tropical Africa (six maps in total from the early 1900s; see Methods and Supplementary Table 1). We estimated current forest extent by subsampling a Landsat-derived global tree cover database²⁷. For calibration of historical extents and modern extent analyses, we used a relatively narrow but meaningful definition of forest as systems that have a closed tree canopy (> 70% tree cover; see Supplementary Fig. 2). In contrast with some other definitions of forest (for example, the Food and Agriculture Organization definition of forest as having > 10% tree cover and including all savannahs²⁸), this definition is meaningful in that it clearly distinguishes open-canopy systems from closed-canopy forests, which are functionally distinct²⁹. However, we also tested the sensitivity of our results to this threshold and

present these results in the Supplementary Information (65 and 75% tree cover; see Supplementary Tables 2 and 3 and Supplementary Fig. 5).

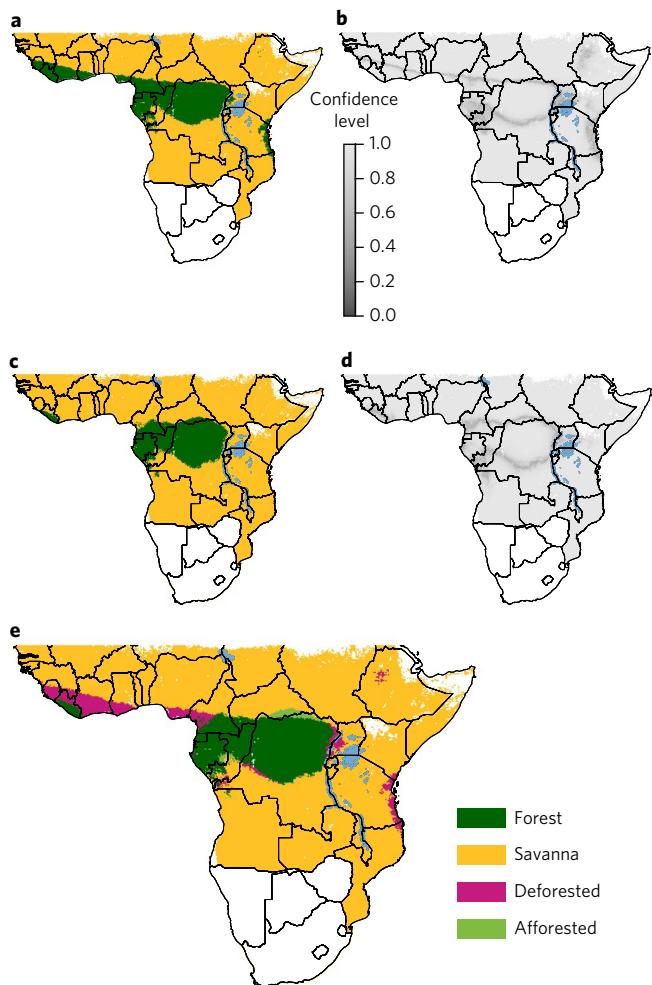
To account for variation in interpretation among these diverse data sources, we used a generalized additive modelling procedure (see Methods) to model both historical and modern forest extent from observations. Generalized additive models deal well with the highly nonlinear, non-monotonic responses to explanatory variables³⁰ that characterize savannah–forest systems—in this case, precipitation, soil characteristics and distance to rivers and, to account for spatial correlations among observations, latitude and longitude.

Results and discussion

We found that forests were historically (around AD 1900) more restricted in tropical Africa (Fig. 2a) than previously estimated^{1,4,15} (Table 1), which was unsurprising given that past studies have largely ignored the potential role of vegetation–fire feedbacks in expanding savannah distributions^{16,17} and sometimes used very loose definitions of forests³¹. Our modelling approach reproduced the current forest extent well using equivalent sampling densities (Fig. 2c and Supplementary Fig. 4), which suggests that the sample sizes of modern and historical forests were sufficient to accurately reproduce forest extent. The net result is a revised map of forest expansion and deforestation that differs substantially from past estimates (Fig. 2e and Table 2)^{7,10,12,14}.

Overall, we estimate a total net loss in forest extent of ~21.7% (95% confidence intervals: 20.9 and 23.2% loss, respectively) between AD 1900 and AD 2000 (Table 2), which is much less than the 35–55% forest loss (Table 1) that has been widely cited^{10,11,31}. Changes in forest cover were heterogeneous; West and East African forests are gone or nearly gone (net loss of ~83.3% in West Africa and ~93.0% in East Africa), but the core Congolese forest extent in Central Africa has increased by ~1.4% on average, with some regions in Central Africa losing and others gaining closed-canopy forests (Fig. 2, Supplementary Fig. 5 and Tables 2 and 3).

These empirical tropical forest extent and change estimates represent a major departure from existing bioclimatic model estimates. Deviations from previous deforestation estimates in West Africa (our estimate of 83.3% instead of ~90%¹² or 29.5%³²; see Table 1), Central Africa (+1.4% instead of −47.8%³³) and even all of tropical Africa (−21.7% instead of −35 to −55%; see Table 1) mostly arise



because previous estimates were primarily bioclimatic⁹ or based on less meaningful definitions of forest^{8,32}. If anything, our estimates may actually under-represent small forest remnants, especially in heavily deforested East and West Africa. Closed-canopy forests currently persist in forest remnants within a human-modified matrix in coastal East Africa, the Eastern Arc Mountain¹³, Ethiopian montane forests³⁴ and Ghana and Côte d'Ivoire²⁷, none of which show up in our current forest extent estimates. As a result, the deforestation estimates proposed here may represent a slight over-estimate of regional-scale deforestation rates (Table 2).

However, despite deviations from previous estimates (Table 1), these revised regional-scale reconstructions are nonetheless consistent with the published empirical literature. Anecdotal historical accounts^{8,24} and localized studies based on historical maps^{8,13} all suggest that European timber merchants harvested most of the commercially valuable timber trees from West and Coastal East African forests during the early 1900s. Biogeographic work also corroborates West and East African coastal forest reconstructions³⁵.

Table 2 | Estimated historical and current forest extent and forest change in tropical Africa

Region	Forest area in AD 1900 (km ²)	Forest area in AD 2000 (km ²)	Absolute change in forest area (km ²)	Relative change in forest area (%)
Central Africa ^a	2,033,920 (2,020,819; 2,051,684)	2,061,729 (2,044,695; 2,067,872)	28,460 (−8,050; 51,155)	+1.4 (−0.4; 2.6)
East Africa ^b	370,681 (334,235; 413,552)	25,645 (21,812; 33,339)	−329,465 (−371,447; −293,222)	−93.0 (−94.7; −91.5)
West Africa ^c	716,646 (691,019; 735,649)	123,428 (115,884; 137,307)	−593,360 (−605,519; −582,242)	−83.3 (−83.8; −81.4)
Tropical Africa (total)	3,527,307 (3,485,929; 3,555,381)	2,760,003 (2,733,684; 2,781,064)	−1,367,234 (−1,476,528; −1,282,952)	−21.7 (−23.2; −20.9)

Associated 95% confidence intervals of the estimates resulting from a bootstrapping procedure are provided in brackets. ^aCameroun, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon and Angola. ^bBurundi, Ethiopia, Kenya, Rwanda, Somalia, Sudan, South Sudan, Tanzania and Uganda. ^cSenegal, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin and Nigeria.

For example, the distribution of mammals, birds and reptiles in the Dahomey Gap in Benin and Togo is consistent with a relatively old disjoint forest distribution³⁵, rather than with a recent deforestation event³⁶, and palaeo-data confirm that the region probably transitioned to savannah ~4,000 years ago as a result of a drying event, which persisted due to feedbacks with fire even after rainfall increased again¹⁷.

In contrast with other regions, the core Congolese forest in Central Africa has experienced net forest expansion over savannahs (Fig. 2 and Table 2). This represents a major departure from previous estimates (from bioclimatic models; see Table 1), but, again, our estimates are in fact consistent with the local literature from the region. Historical studies have repeatedly documented widespread forest encroachment into savannah during the past century in Central Africa^{37,38}. A particularly striking example is the city of Yaoundé, Cameroun, which was located at the savannah–forest boundary in 1913 (ref. ³⁹), but is now much deeper in the forest interior (Fig. 2). Place names suggest a similar pattern throughout Central Africa: villages that are now surrounded by forests are still named after savannahs. The southern Congo has been less well documented (the region is generally less studied); forest expansion may represent another real trend towards forested encroachment of savannah, or may be an artefact either of low accuracy of the historical maps⁴⁰ (see Supplementary Fig. 3) or biased remote sensing estimates of current forest extent³. However, at least in recent decades, remote sensing analyses and in situ measurements have documented widespread forest progression^{41,42}. Moreover, biogeographic data independently confirm the pattern; areas that are being encroached by forests generally do not fall within the Congolian biogeographic region, but rather form part of diverse savannah biogeographic regions³⁵.

In total, forests have encroached more than ~135,270 km² of savannahs in tropical Africa during the past century. The drivers of this forest expansion are a matter of some debate. Forest expansion may reflect a colonial policy of fire suppression³⁶. Alternatively, savannah and forest responses to palaeoclimatic variation may occur slowly via spatial processes (J.C.A. & A.C.S., manuscript in preparation); forests may have begun encroaching savannahs when rainfall increased and seasonality decreased following the Holocene crisis ~3,000 BP, a process which may not yet be complete⁴³.

Another possibility is that the vegetation is responding to the increase in atmospheric CO₂, which may favour C₃ trees over C₄ savannah grasses, leading to forest expansion⁴⁴. Regardless, forests are eroding mesic, biogeographically unique savannahs in Central Africa³⁵, with critical implications for the conservation of these relatively poorly protected systems¹⁸. Afforestation proposals for climate change mitigation may seriously aggravate this ongoing trend. Using only bioclimatic variables, a variety of organizations have erroneously identified tropical mesic savannahs where forests are climatically possible as degraded systems and thus as possible targets for biofuel production²⁰ or 'reforestation'¹⁹.

Localized but regionally slow deforestation of core Congolese forest makes these forests a global anomaly compared with forests in other African regions and throughout South America and Asia, where deforestation has been much more rapid. Slow deforestation likely reflects the particular history of the region. Congolese forests were populated and extensively cultivated before European colonization⁴⁵, but colonization concentrated people and villages along roads and in open environments⁴⁵, potentially alleviating the effects of shifting cultivation. A recent history of severe post-colonial conflicts likely also contributes to slower deforestation, since violent conflicts can prevent the infrastructure investments necessary to make large-scale logging and agriculture feasible^{46,47}.

Conclusions

Here, we present a continental-scale empirical attempt to reconstruct pre-colonial tropical forest extent in tropical Africa. Forests in tropical Africa were historically less extensive than existing bioclimatic models suggest^{14,15}, and mesic savannahs were probably widespread even before modern agricultural expansion. As a result, deforestation rates in tropical Africa have been over-estimated; our estimates suggest a continental deforestation rate since AD 1900 of ~21.7% instead of 35–55% (Table 1). Nonetheless, the net tropical African deforestation exceeds deforestation rates in Amazonia (11.4% total¹⁰) but not in Southeast Asia (25%¹¹). Integrating these estimates for forest area losses with recent estimates of African aboveground forest biomass stocks⁴⁸, we estimate that land-use change may have contributed ~27 ± 2 Pg of aboveground carbon to the global atmosphere between AD 1900 and AD 2000 (at a rate of 0.27 Pg per year). This estimate is, of course, associated with uncertainties: aboveground biomass estimates are derived from modern plots, which may not correspond to past forest biomass due to changes in land use¹³ or CO₂ fertilization⁴⁴, and are not differentiated here into different forest types. Nonetheless, these revised forest extent and deforestation rates will change our understanding of a range of processes, from deforestation contributions to the global carbon cycle over the past century to conservation and livelihoods within tropical savannahs.

Methods

Data. *Bio-proxies.* To infer recent past vegetation (around AD 1900) in tropical Africa, we performed a meta-analysis of 180 published records of fossil pollen, phytoliths, δ¹³C soil organic matter records and charred material (Supplementary Data 1). We identified these studies through a literature search using Google Scholar (<https://scholar.google.com>) for the following keywords: 'palaeo' AND 'vegetation' AND 'Africa' AND either 'pollen', 'phytoliths', 'δ¹³C' or 'macro-remains' to represent each proxy type. Palaeo-proxies are preserved in sedimentary archives, such as lake sediments and palaeosols, and are commonly used to reconstruct past vegetation:

1. AP/NAP. The ratio of arboreal (AP) to non-arboreal (NAP) pollen is commonly used to provide information that allows us to distinguish wooded from more open ecosystems⁴⁹ and has been quantitatively calibrated against tropical woody cover⁵⁰. We included pollen data from a total of 85 sites^{51–110}, selecting sites that were dated between 1850 and 1920. We classified pollen types as AP and NAP following the classification of Vincens et al.¹¹¹ for trees and shrubs and JSTOR for others (<http://plants.jstor.org/>) and then computed the AP-to-NAP ratio for each record (Supplementary Data 1).
2. D/P. Phytoliths are increasingly used in tropical environments, where they differentiate some plant taxa whose pollen do not permit classification to

sufficient taxonomic resolution; for example, among the Poaceae (P)¹¹². The ratio of woody dicotyledons (D) to P phytoliths has been used successfully to reconstruct woody cover^{50,113}. Three of the eleven phytolith records were derived from lake sediments¹¹⁴ and eight from soil profiles^{115–117}. For lake sediment sites, data were extracted from the level corresponding to around AD 1900 (Supplementary Data 1); for the soil profile sites, ages were inferred from the first dated level. We computed the D/P index as the ratio of globular granulate and decorated morphotypes over the sum of grass silica short cells^{50,114,118}.

3. Soil δ¹³C. The δ¹³C value of soil organic matter can be used to estimate the relative abundance of trees and grasses in tropical environments, because it reflects the relative contributions to carbon fixation of the C₃ and C₄ photosynthetic pathways used by tropical trees and grasses, respectively¹¹⁹. We included 49 soil carbon records^{37,38,120–124}.
4. Charcoal. Dated charred materials can also be used as proxy for local past vegetation¹²⁵. We included 37 records of charred macro-remains categorized by the authors as indicative of either savannah or forest^{125–132}.

Calibration for past biome attribution. Reconstructing vegetation from bio-proxies data requires calibration. To calibrate each palaeo-proxy against current vegetation type, we performed a meta-analysis of published modern samples of pollen, phytoliths and soil organic matter δ¹³C. We used modern pollen data from the African Pollen Database (<http://fpd.sedoo.fr/fpd/>). Because samples were more numerous in savannah than forest, we subsampled the same number of samples from each biome ($n = 200$ for each one). We gathered 247 modern phytoliths samples^{30,113,116,117,133–139} (Supplementary Data 2) and computed the D/P index for each. Finally, we assembled 84 samples^{37,38,50,117,120,124,140} of modern δ¹³C with each modern sample defined as the first 10 cm of soil profile (Supplementary Data 3).

We calibrated modern palaeo-proxy data against biome distribution. For phytoliths and δ¹³C, we used the vegetation description from each publication itself (see Supplementary Data 2 and 3). To attribute a biome for each modern pollen sample, we used a map of the forest and savannah distribution derived from the Landsat tree cover dataset²⁷ (see 'Modern forest distribution'). We used fitted recursive partitioning classification trees to define the threshold of proxies indices attributed to savannah versus forest, using the *rpart* package in the R statistical programme¹⁴¹. The three calibration functions accurately predicted forest and savannah, with 73, 98 and 93% of accurate predictions, respectively, for AP/NAP, D/P and δ¹³C. We applied the calibration functions to fossil data and, for each reconstructed biome type, we compared interpretations made by the authors for confirmation (Supplementary Data 1).

Historical maps. To supplement the palaeo-proxy data, we performed a literature search (Google Scholar with the keywords 'historic map' AND 'forest' AND 'Africa'; 'vegetation map' AND '1900' AND 'Africa'; 'Forest map' AND '1900' AND each region of Africa) and targeted essays and documents published from identified key explorers in French, German, Portuguese and English, dating back to the beginning of the twentieth century. We found six maps suitable for our analysis (Supplementary Table 1): a map with the location of the 'great Forest' in the eastern part of the present-day Democratic Republic of Congo from Henry Morton Stanley's travels¹⁴², a map of vegetation types in East Africa by A. Engler and O. Drude¹⁴³, a map of forest cover in West Africa by Auguste Chevalier¹⁴⁴, a map of Cameroon with the delineation of the forest–grassland boundary by Max Moisel¹⁴⁵, a map of the Equatorial forest of Central Africa by Meunier¹⁴⁶ and finally a vegetation map of Africa by Shantz and Marbut⁴⁰ for the southern part of the Congo Basin, the East African Coastal Forest and the Ethiopian Mountainous forest.

We digitized and georeferenced each of the six maps in QGIS version 2.18 (<http://qgis.osgeo.org>). For georeferencing, we used control points of known coordinates (national borders, coastlines, locations of villages and other identifiable features of known coordinates) and applied a first-order polynomial transformation based on a least-squares fitting algorithm¹³. The maps were projected into a World Geodetic System 1984 geographic coordinate system. For each map, the vegetation classification was different, and thus we classified them into two land cover categories: forest versus other open ecosystems, including all ecosystems belonging to the savannah spectrum (see vegetation distinction in Supplementary Table 1). We then digitized areas of forest cover to create the vectors corresponding to the forest land cover type (see Supplementary Fig. 1).

Historical maps also come with uncertainty regarding the production of the map and the accuracy of georeferencing at the time of the map design¹³. To evaluate the spatial accuracy of each historical map, we selected a number of permanent geographical features, such as towns, and measured the distance between the location of this feature on the historical map and on a reference map (Supplementary Table 1). The distances for each of the selected features were then interpolated using an inverse distance weighting¹⁴⁷ to create maps of spatial errors for each of the historical maps (see Supplementary Fig. 3).

Modern forest distribution. To define the distribution of modern tropical forest, we used the Landsat-derived tree cover for the year AD 2000 (ref. ²⁷), which provides spatially explicit data at a 30 m resolution, corresponding to tree cover of trees with a height of > 5 m. This product is widely used to differentiate between

closed-canopy forest and open-canopy savannah ecosystems¹⁶, as the boundary between the two ecosystems is characterized by an abrupt change in tree cover. We therefore computed the histogram and estimated the probability density of tree cover and we defined the tree cover frequency minimum of 70% as the threshold between savannah and forest (Supplementary Fig. 2). The delineation of forest using remote sensing products, and thus the threshold of tree cover used to differentiate between forest and savannah ecosystems, is still debated¹. To explicitly address this debate and to test the sensitivity of the methodological framework to the choice of the tree cover threshold, we tried both 65 and 75% tree cover thresholds; we present these additional results in Supplementary Tables 2 and 3 and Supplementary Figs. 5–7.

Environmental data. Historical (PrecipH) and modern (PrecipM) precipitation data were obtained from the Climatic Research Unit (release of CRU TS3.21), which contains historical monthly precipitation data for global land areas from AD 1900, gridded at 0.5° latitude/longitude resolution¹⁴⁷. Precipitation data were interpolated from monthly observations at over 4,000 meteorological stations across the world's land areas¹⁴⁷. To best reflect the historical and current precipitation, we computed the average of 1901–1910 annual precipitation for historical conditions and the average of 1995–2004 annual precipitation for modern conditions.

Soil data were obtained from the International Soil Reference and Information Centre World Soil Information team in collaboration with the African Soil Information System project (www.isric.org; soil map of Africa at 1 km resolution). We considered sand content of the top 30 cm (SandT) and bottom 100–200 cm (SandB) of the soil profile. It is unlikely that the sand content has changed over the past century. We therefore used the same estimates of SandT and SandB to model both historical and modern forest distribution.

We also included distance to rivers (DistR; from <http://www.openstreetmap.org>) as a model covariate. All variables were centred and normalized to a mean of 0 and a standard deviation of 1 before analysis.

Statistical analysis. Model. We modelled the historical and modern forest distribution using generalized additive models with smoothness estimation using penalized regression splines. The strength of generalized additive models is their ability to deal with highly nonlinear and non-monotonic relationships between the response and the set of explanatory variables and thus generate accurate probabilistic estimates of the response variable³⁰. Generalized additive models allow for the dependence of the response on the predictors to be represented as a parametric sub-model plus the sum of smooth functions of one or more of the predictor variables. All models were run using the function *gam* from the *mgcv* package in statistical software R (version 3.1.2; ref. ¹⁴¹). We used package 'AUC' to calculate the area under the receiver operating curve (AUC) to measure model predictive accuracy. The AUC is a measure of classifier performance that balances sensitivity (true positive rate) against (1 – specificity) (false positive rate)⁴⁸. The AUC values lie between 0.5 and 1, where 0.5 denotes a bad classifier and 1 denotes an excellent classifier.

Models were fitted to historical and modern data based on equivalent sample sizes. To balance the 180 palaeo-proxy sites with data from historical maps, we randomly selected 360 data points from historical maps, bringing the total sample size to 540. To estimate the modern forest extent based on an equivalent sample size, we randomly subsampled 540 points from the Landsat-tree-cover-derived forest distribution³⁷. Historical and modern forest extents were modelled as binomial random variables with a single model with unique smoothing terms that depended on time (here, using the historical and modern forest extent as categorical factors). This was accomplished by using the term 'by' in the model equation, resulting in separate estimates and patterns of variation for each temporal period. Forest extent was modelled as a function of smoothed and time-dependent terms of PrecipH (for historical forest distribution) and PrecipM (for modern forest distribution), and smoothed terms of SandT, SandB and DistR. To account for spatial dependence among observations, smoothed and time-dependent terms of latitude and longitude were also fitted. Using the logit link $\log(p/(1-p))$, the model structure was as follows:

$$\begin{aligned} \text{logit(Forest)} = & \beta_0 + f_{\text{Precip}}(\text{Precip}, \text{by} = \text{time}) \\ & + f_{\text{Lat,Lon}}(\text{Lat}, \text{Lon}, \text{by} = \text{time}) \\ & + f_{\text{SandT}}(\text{SandT}) + f_{\text{SandB}}(\text{SandB}) \\ & + f_{\text{DistR}}(\text{DistR}) \end{aligned}$$

where β_0 is the intercept and f stands for the smoothing terms for the respective model variables. We set the degree of smoothness of model terms with a smoothing parameter $k = 30$. The choice of $k = 30$ ensured enough degrees of freedom to represent the underlying true relationships reasonably well, but nonetheless maintained reasonable computational efficiency.

We ran three sets of models based on a 65, 70 and 75% tree cover threshold (only the results for the 70% threshold are presented in the main text, while the results for the 65 and 75% thresholds are presented in the Supplementary Information). For each set, we ran 1,000 individual models. The final probabilistic estimate of forest extent for each model set was obtained by considering the ensemble of all 1,000 models and calculated by taking the median of

the probabilistic estimates from the individual models (hereafter, 'ensemble probabilistic estimate'; Supplementary Fig. 7).

Forest and savannah extent and change estimate. To ease the interpretation of the results and aid conservation decisions, we derived the forest–savannah biome boundary in addition to the ensemble probabilistic estimates of forest and savannah extent. We chose a threshold probability value of 0.5 as an indicator of the biome boundary and designated all cells with a probability (of being a forest) of > 0.5 as forest and those with values ≤ 0.5 as savannah. Using the forest extent estimates resulting from applying that threshold, we then estimated the change in forest cover between AD 1900 and AD 2000 and deforestation rates for each country and region (West, East and Central) in Africa, as well as for all of tropical Africa. Changes were calculated with reference to the estimated historical forest extent and were shown as the percentage change. Change estimates obtained using the 70% tree cover threshold are shown in the main text, while those obtained using 65 and 75% tree cover thresholds are shown in the Supplementary Information.

Confidence level estimates. To quantify the uncertainty of the biome boundary estimate, we computed the proportion for which the probabilistic estimate in the 1,000 individual models was > 0.5 . For example, if 900 of the 1,000 individual models indicated that a given location was forested and that location was designated as forest using the threshold probability value of 0.5, the confidence estimate for that location was 0.9 (Supplementary Fig. 6).

The uncertainty of the forest change estimate was assessed using a bootstrapping procedure. We randomly (with replacement) selected 100 historical and modern forest extent estimates and quantified the median deforestation rate between AD 1900 and AD 2000 for these 100 modelled estimates using the methods discussed above (see 'Forest and savannah extent and change estimate'). We repeated this procedure 100 times and obtained the 2.5 and 97.5 quantile confidence intervals. We performed this bootstrapping procedure to obtain confidence intervals for each country and region (West, East and Central) in Africa, as well as for all of tropical Africa.

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. All data and R code used to generate past forest extent are provided in the Supplementary Information. The raster data of past and present forest extent are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.r87p0>) with request to cite the present paper when using the data.

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Author contributions

J.C.A. and A.C.S. designed the study and analyses. J.C.A. assembled and calibrated the palaeo-data. M.A.J. developed and ran the models. J.C.A. and A.C.S. co-wrote the paper, with feedback and methods contributions from M.A.J.

Competing interests

The authors declare no competing financial interests.

Additional information

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► Experimental design

1. Sample size

Describe how sample size was determined.

To balance the 180 paleo-proxy sites with data from historical maps, we randomly selected 360 data points from historical maps (more spatially explicit data), bringing the total sample size to 540. To estimate modern forest extent based on an equivalent sample size, we randomly subsampled 540 points from the Landsat tree cover derived forest distribution. The sample size was determined as sufficient to reproduce forest extent due to the good agreement between modeled and empirical data (Supplementary Figure 4, AUC results).

2. Data exclusions

Describe any data exclusions.

No data were excluded from the analyses.

3. Replication

Describe whether the experimental findings were reliably reproduced.

NA

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

NA

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

NA

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

We used the open software R to analyze the data. We used R packages "gam" and "mgcv" to run models.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). [Nature Methods guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

All the raw data, results (rasters) and R codes are available without restrictions. The input data (from bio-proxies) and R codes are available in the Supplementary Information, and the rasters are available from the authors and from Dryad.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

NA

10. Eukaryotic cell lines

- State the source of each eukaryotic cell line used.
- Describe the method of cell line authentication used.
- Report whether the cell lines were tested for mycoplasma contamination.
- If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

NA

NA

NA

NA

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

NA

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

NA