Received: 9 December 2019 | Revised: 9 November 2020 | Accepted: 12 November 2020

DOI: 10.1111/jbi.14051

RESEARCH ARTICLE

Journal of Biogeography | WILEY

Plastid introgression and evolution of African miombo woodlands: New insights from the plastome-based phylogeny of *Brachystegia* trees

Arthur F. Boom[1] | Jérémy Migliore[1,2] | Esra Kaymak[1] | Pierre Meerts[3] | Olivier J. Hardy[1]

[1]Service Evolution Biologique et Ecologie, Faculté des Sciences, Université Libre de Bruxelles, Bruxelles, Belgium

[2]Muséum départemental du Var, Toulon, France

[3]Service Ecologie végétale et Biogéochimie, Faculté des Sciences, Université Libre de Bruxelles, Bruxelles, Belgium

Correspondence
Arthur F. Boom, Service Evolution Biologique et Ecologie, Faculté des Sciences, Université Libre de Bruxelles, CP 160/12, 50 avenue F.D. Roosevelt, 1050 Brussels, Belgium.
Email: boomarthur@gmail.com

Funding information
Belgian Federal Science Policy Office, Grant/Award Number: BRAIN.be BR/132/A1/AFRIFORD; Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture

Handling Editor: Felix Forest

Abstract

Aim: Miombo woodlands form a characteristic vegetation type covering 2.7 million km^2 in southern and eastern Africa. Despite their wide geographical extent, their origin, floristic and spatial evolution through time remain understudied. To fill this gap, we studied the evolution of *Brachystegia* trees, one of the most representative genera of these woodlands (20 species), also represented in Guineo-Congolian rain forests (8 species).

Location: Tropical Africa, Guineo-Congolian forests and Zambezian savannas.

Taxon: *Brachystegia* genus.

Methods: We used a genome skimming approach to sequence the plastomes of 45 *Brachystegia* samples, covering 25 of the 29 existing species, and one outgroup (*Julbernardia paniculata*). The phylogeny of the plastomes was reconstructed and time-calibrated. We tested if the genetic divergence between lineages reflected taxonomic and/or geographical distances using Mantel tests. Finally, we inferred the evolutionary history of *Brachystegia* based on the age and spatial distribution of its lineages.

Results: Surprisingly, species represented by multiple specimens appear rarely monophyletic while plastid clades display strong geographical structuring, independently of the species. Two main clades separate woodland and rain forest species, which diverged during the late Miocene–Pliocene (95% HPD = 2.78–8.59 Ma). In miombo woodlands, three subclades occur in parapatry along an East–West axis, ranging from Angola to East Africa. Their divergence started from the Plio-Pleistocene (95% HPD = 1.17–3.69 Ma). Divergence dates (TMRCA) within miombo subclades decrease from East Africa (1.53 Ma) to Angola (0.76 Ma).

Main conclusions: *Brachystegia* plastomes appear unreliable to identify species, probably due to species introgression leading to recurrent chloroplast captures. However, they prove very informative for tracking the past dynamics of the genus, and suggest a historical westwards expansion of miombo *Brachystegia*, and possibly of miombo vegetation, during the Plio-Pleistocene. Further investigations using nuclear DNA

are needed to assess the species tree as well as speciation and hybridization events between species.

KEYWORDS

Brachystegia, chloroplast capture, miombo woodlands, molecular phylogeny, plastome, savanna

1 | INTRODUCTION

Miombo woodlands are dry tropical woodlands occurring in southern and eastern tropical Africa and are dominated by trees from the genus *Brachystegia* (in Swahili, *Myombo* is the common name given to trees of this genus). They form a vegetation belt covering c. 2.7 million km^2 from Angola to Tanzania (Frost, 1996), globally reflecting the Zambezian regional centre of endemism, which is the largest African phytochorion (White, 1986). Miombo are referred non-exclusively to as savannas (Pennington et al., 2018), woodlands, and/or dry forests (Frost, 1996; Prance, 2006; Timberlake et al., 2010), depending on authors and definitions considered. As stated by Campbell et al. (1996), a convenient way to describe miombo over most of its range could be as physiognomically closed deciduous woodlands within the spectrum of savanna ecosystems. Miombo woodlands grow on nutrient-poor soils, with a closed but not overly dense canopy, allowing the growth of an herbaceous layer (Frost, 1996). Mean annual rainfall ranges from 650 to 1,400 mm, marked by a seasonal drought period (Campbell et al., 1996). Fire regime is one key driver of miombo, as fire frequency and intensity are responsible for converting woodlands to open grasslands or dry forests (Furley et al., 2008; Schmitz, 1962; Trapnell, 1959). Floristically, the most striking feature of miombo is the canopy dominated by Legumes of the subfamily Detarioideae, particularly *Brachystegia*, *Isoberlinia* and *Julbernardia* (de la Estrella et al., 2018; Frost, 1996).

Woodlands physiognomically similar to miombo did exist as far as the middle Eocene, even if they probably differed in species composition (Jacobs & Herendeen, 2004). Savanna occurrences have been documented since the end of the Early Miocene (c. 16 Ma) in West Africa (Morley & Richards, 1993), but expansion of C4 fire-prone savannas in Africa occurs around 8–10 Ma (Cerling, 1992; Morley & Richards, 1993; Polissar et al., 2019), synchronously with other C4 grasslands across the globe (Beerling & Osborne, 2006). Before the Plio-Pleistocene, C4 savannas represented a marginal part of the biomass (Cerling, 1992). Miombo woodlands have floristic affinities with other types of African savannas (Daru et al., 2018; Fayolle et al., 2019) but also with Guineo-Congolian forests, since several tree genera are shared, such as *Afzelia*, *Brachystegia*, *Isoberlinia* and *Uapaca* (Donkpegan et al., 2017; Linder, 2014; Radcliffe-Smith, 1993). To explain such biogeographical links, phylogenetic reconstructions within the genera *Guibourtia* (Tosso et al., 2018) and *Entandrophragma* (Monthe et al., 2019), and the tribe Melastomateae (Veranso-Libalah et al., 2018), revealed diversification events associated with biome shifts from close forested to more open habitats during the Miocene–Pliocene. Similarly, the woody flora of Brazilian savanna, that is, cerrados *sensu lato*, seems to have evolved from more forested biomes since 10 Ma, with most of the diversification reported after 5 Ma (Simon & Pennington, 2012). However, at the interface between African rain forests and open grasslands, the origin and evolution of miombo landscapes remain elusive, as emphasized by Linder (2014).

Among the main representative trees of miombo, *Brachystegia* Benth. is by far the most diverse genus, with 20 of its 29 recognized species reported in these woodlands (Lebrun & Stork, 2008), including trees, shrubs and suffrutex life-forms. Within the miombo belt, Zambia constitutes the diversity centre of the genus, whereas drier miombo and woodlands on Kalahari sands are less rich in species (Frost, 1996; White, 1986). Additionally, eight *Brachystegia* species are found in the Guineo-Congolian rain forests, and *B. oblonga* grows in coastal Mozambique forest. The taxonomy of this tropical genus is notoriously difficult, as the species are morphologically variable (Chikuni, 1998). Additionally, *Brachystegia* species from miombo woodlands seem prone to hybridization, with 14 hybrids recognized by Arthur C. Hoyle from field and herbarium observations (White, 1962). This view is, however, challenged, as morphometric and preliminary genetic analyses poorly supported this hybridization pattern (Chikuni, 1998).

Phylogenetic methods are well suited for understanding how and when biomes have established through time, since the climatic niche of species is generally a phylogenetically conserved trait (Pennington et al., 2006). Reconstructing a well-resolved and dated phylogenetic tree for *Brachystegia* is, therefore, promising to gain insight into the biogeographical history of miombo woodlands. In this context, genome skimming is a cost-effective and shallow sequencing approach allowing to assemble DNA regions occurring in high copy number by multiplexing numerous samples in the same sequencing run (Hollingsworth et al., 2016). By sequencing short reads, still available in samples with degraded DNA, genome skimming has been successfully applied to sequence plastomes from herbarium samples (Bakker et al., 2016), reaching thus a good taxonomic and geographical cover, as some taxa could be rare and/or geographically restricted and therefore difficult to collect (Savolainen et al., 1995). Whole plastome data usually lead to highly resolved phylogenetic trees, even within genera or species, and are therefore very informative to reconstruct past colonization events and phylogeographical history (e.g. Demenou et al., 2020; Migliore et al., 2019; Monthe et al., 2019; Tosso et al., 2018; for examples of African trees).

Nevertheless, at the interspecific level, plastid phylogenies are sometimes very discordant with phylogenies of nuclear genes, due to incomplete lineage sorting or selection processes, or when occasional

hybridization events led to plastid capture (Rieseberg & Soltis, 1991). The latter is expected to occur more frequently between related species during range shifts whenever plastomes are dispersed over much shorter distances than nuclear genes (Petit & Excoffier, 2009), for example because of asymmetric seed versus pollen dispersal capacities. In this case, the distribution of plastid lineages could be better explained by geography than by taxonomy, as often observed for example in the genus *Quercus* (e.g. Pham et al., 2017; Simeone et al., 2018). It is thus necessary to control whether plastid phylogenies are globally consistent with species delimitation to interpret correctly the evolutionary processes they represent.

Here, we investigate the diversification of *Brachystegia* trees to gain insights into the origin and evolution of miombo woodlands. To this end, we use genome skimming to sequence the plastomes of 45 samples covering the distribution range of the genus and representing 25 of the 29 species. Applying phylogenetic and molecular dating approaches, we will address the following biogeographical questions:

1. Is plastid phylogeny consistent with species delimitation or, alternatively, does it display a strong geographical structure across species boundaries? Here we contrast three alternative hypotheses. H1: Species are well delimited, do not introgress and coalescence rate was high enough so that they appear as monophyletic entities. H2: Species do not introgress but incomplete lineage sorting due to large effective population sizes and/or limited divergence time led to shared polymorphism (non-monophyly), without geographical signal. H3: Recurrent introgression and chloroplast captures among species led to a strong phylogeographical pattern whereby co-occurring individuals from distinct species tend to share the same lineages, and species are not monophyletic unless they are geographically isolated.
2. Is there evidence of one or several evolutionary transitions between rain forest and miombo and in which direction(s)? We propose the following hypotheses. H4: The ecological niche is fairly conserved and only one biome shift occurred. H5: Biome shift occurred from rain forest to miombo, following the general trend of aridification and rain forest reduction that occurred over the last 50 Ma (Kissling et al., 2012).
3. What can we learn from the timing of divergence of plastid clades about diversification, biome shift(s) and/or range shifts? Here, we hypothesize (H6) that the diversification of miombo species was concomitant with the development of C4 fire-prone savannas during the Miocene.

2 | MATERIALS AND METHODS

2.1 | Sampling strategy

Plant material was collected on 109 vouchers from the following herbaria: BR (Meise Botanic Garden, Belgium), BRLU (Université Libre de Bruxelles, Belgium), FHO (Daubeny Herbarium, University of Oxford, UK) and LISC (Instituto de Investigação Científica Tropical, Lisboa, Portugal). Silica-dried leaves from 86 individuals were also collected in D. R. Congo, and vouchers deposited at BRLU.

We seek to obtain two or three samples per *Brachystegia* species but given the rarity of some species in herbarium collections and the low DNA content (c. 27% of the herbarium vouchers tested contained less than 1 ng of DNA per μl), we eventually retrieved sufficiently good quality DNA for 45 individuals (1–3 individuals per species; Table 1) representing 25 of the 29 described species of *Brachystegia* (following Lebrun & Stork, 2008). A sample of *Julbernardia paniculata* was added as an outgroup to anchor the phylogeny.

2.2 | DNA extraction and genomic libraries preparation

DNA was extracted from herbarium samples following the protocol of Cappellini et al. (2010) with slight modifications: no initial wash step with a bleach solution and overnight digestion at 37°C rather than 55°C. For the recent silica-dried material collected in the field, DNA extraction was performed using the DNeasy Plant Mini Kit (Qiagen), following the manufacturer's recommendations. DNA quality and its level of fragmentation were checked on 1% agarose gels, before quantification with a Qubit® 2.0 Fluorometer (Life Technologies, Invitrogen). DNA with a low level of fragmentation (i.e. absence of smear and most of the DNA longer than 1,000 bp) were sheared using a Bioruptor® Pico (Diagenode SA.). The program was set to obtain fragments of c. 400 bp.

Genomic libraries were prepared with the NEBNext Ultra II DNA Library Prep Kit (New England Biolabs), and barcoded by dual indexing (8-bp long barcodes) following the Illumina True-Seq protocol. Insert size was set around 250 bp. After pooling, we sequenced them on an Illumina NextSeq 500 instrument at the GIGA platform (Liège, Belgium) using the V2 mid-output reagent kit to produce 2 × 150 bp paired-end reads, targeting more than one million reads per sample.

2.3 | Bioinformatic treatment

After Illumina demultiplexing, all reads were checked using FastQC 0.11.7 (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/) for quality control and determination of adapter content before trimming using Trim Galore! 0.4.5 (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/). A reference plastome for *Brachystegia* was assembled de novo using GetOrganelle 1.6.2 (default parameters for chloroplast assembly; Jin et al., 2019) for *B. bakeriana* (specimen Dechamps, Murta & da Silva 1327 [LISC]). This latter was chosen as the best de novo assembled plastome, among the samples providing the highest number of reads. The resulting assembly was checked with Bandage 0.8.1 (Wick et al., 2015). The inverted repeats were manually oriented by comparison with another Detarioideae plastome (*Afzelia africana*, GenBank accession

TABLE 1 Characteristics of the specimens used for plastome sequencing. Vouchers are hosted in the following institutions: BR (Meise Botanic Garden, Belgium), BRLU (Université Libre de Bruxelles, Belgium), FHO (Daubeny Herbarium, University of Oxford, UK), and LISC (Instituto de Investigação Científica Tropical, Lisboa, Portugal). Four *Brachystegia* species are missing for this study (*B. mildbraedii* Harms, *B. oblonga* Sims, *B. utilis* Hutch. & Burtt Davy and *B. zenkeri* Harms). Coordinates are in decimal degrees. DRC is the abbreviation for the Democratic Republic of the Congo

ID	Taxon	Latitude	Longitude	Collector and collection year	Country	Herbarium and collector number
1	*Brachystegia allenii* Hutch. & Burtt Davy	−10.689	38.945	Milne-Redhead E., Taylor P. (1955)	Tanzania	FHO 7663
2	*Brachystegia allenii* Hutch. & Burtt Davy	−14.960	30.246	White F. (1952)	Zambia	BR 2406A
3	*Brachystegia angustistipulata* De Wild	−6.000	30.000	Jefford T.G., Juniper B.E., Newbould J. (1958)	Tanzania	BR 2799
4	*Brachystegia bakeriana* Hutch. & Burtt Davy	−14.817	18.633	Dechamps R., Murta F. & da Silva M. (1974)	Angola	BR 1327
5	*Brachystegia boehmii* Taub.	−4.832	29.962	Procter J. (1954)	Tanzania	FHO 262
6	*Brachystegia boehmii* Taub.	−11.530	27.467	Boom A. (2016)	DRC	BRLU 38
7	*Brachystegia boehmii* Taub.	na	na	Duvigneaud P. (1957)	DRC	BRLU 2833
8	*Brachystegia bussei* Harms	−14.726	30.762	White F. (1952)	Zambia	BR 2410
9	*Brachystegia bussei* Harms	−6.041	37.519	Burtt B.D. (1933)	Tanzania	BR 4736
10	*Brachystegia cynometroides* Harms	na	na	Forest Product Research Laboratory (1969)	Cameroon	FHO
11	*Brachystegia eurycoma* Harms	7.710	11.480	Latilo M.G., Daramola B.O. (1954)	Nigeria	BR 28945
12	*Brachystegia eurycoma* Harms	7.230	10.628	Chapman H.M. (1974)	Nigeria	FHO 156
13	*Brachystegia floribunda* Benth.	−12.179	17.242	Barbosa L.A.G. (1965)	Angola	LISC 11037A
14	*Brachystegia floribunda* Benth.	−11.530	27.467	Boom A. (2016)	DRC	BRLU 41
15	*Brachystegia gossweileri* Hutch. & Burtt Davy	−10.735	14.981	Barbosa L.A.G. (1965)	Angola	FHO 10988
16	*Brachystegia gossweileri* Hutch. & Burtt Davy	−12.148	18.090	Mendes dos Santos R. (1965)	Angola	FHO 1980
17	*Brachystegia kennedyi* Hoyle	6.105	5.893	Meikle R.D., Keay R.W.J. (1949)	Nigeria	BR 581
18	*Brachystegia kennedyi* Hoyle	6.105	5.893	Kennedy J.D.	Nigeria	FHO 2181
19	*Brachystegia laurentii* (De Wild.) Louis ex Hoyle	−0.974	10.925	Wieringa J.J. (2001)	Gabon	BR 4529
20	*Brachystegia leonensis* Hutch. & Burtt Davy	8.913	−11.728	Sesay J.A. (2010)	Sierra Leone	BR 51
21	*Brachystegia leonensis* Hutch. & Burtt Davy	5.646	−8.135	Jongkind C.C.H. (2010)	Liberia	BR 9067
22	*Brachystegia longifolia* Benth.	−10.915	28.517	Boom A. (2016)	DRC	BRLU 37
23	*Brachystegia longifolia* Benth.	−11.983	18.283	Dechamps R., Murta F. & da Silva M. (1974)	Angola	BR 1400
24	*Brachystegia longifolia* Benth.	−11.530	27.466	Boom A. (2016)	DRC	BRLU 39
25	*Brachystegia manga* De Wild.	−7.623	33.403	Groome C. & Hoyle A.C. (1949)	Tanzania	FHO 1073

(Continues)

TABLE 1 (Continued)

ID	Taxon	Latitude	Longitude	Collector and collection year	Country	Herbarium and collector number
26	*Brachystegia manga* De Wild.	−11.187	27.905	Duvigneaud P. (1948)	DRC	BR 1214
27	*Brachystegia michelmorei* Hoyle	−9.796	29.295	Astle W. L. (1965)	Zambia	FHO 797
28	*Brachystegia microphylla* Harms	−4.485	35.758	Leippert H. (1966)	Tanzania	BR 6334
29	*Brachystegia nigerica* Hoyle & A.P.D. Jones	6.155	6.770	Chesters D.F.	Nigeria	BR A124/30
30	*Brachystegia nigerica* Hoyle & A.P.D. Jones	7.134	3.840	Lapido J.L. (1946)	Nigeria	FHO 19061
31	*Brachystegia puberula* Hutch. & Burtt Davy	−14.217	14.033	Bamps P., Martins S. & Matos C. (1973)	Angola	BR 4473
32	*Brachystegia russelliae* I. M. Johnst.	na	na	Mendes E.J. (1955)	Angola	BR 55
33	*Brachystegia russelliae* I. M. Johnst.	−12.476	16.295	Mendonça F.A. (1965)	Angola	FHO 4593
34	*Brachystegia spiciformis* Benth.	−5.863	23.392	Liben L. (1956)	DRC	BR 1742
35	*Brachystegia spiciformis* Benth.	−11.488	27.600	Boom A. (2016)	DRC	BRLU 61
36	*Brachystegia spiciformis* Benth.	−10.598	22.345	Duvigneaud P., Timperman J. (1956)	DRC	BRLU 2423 B2
37	*Brachystegia spiciformis* Benth.	−14.831	13.621	Barbosa L.A.G., Henriques C., Moreno F. (1967)	Angola	BRLU 2164
38	*Brachystegia stipulata* De Wild.	−11.510	28.007	Boom A. (2016)	DRC	BRLU 7
39	*Brachystegia tamarindoides* Welw. ex Benth.	−10.693	23.182	Duvigneaud P., Timperman J. (1956)	DRC	BRLU 2317
40	*Brachystegia tamarindoides* Welw. ex Benth.	−15.096	13.565	Torre A.R. (1956)	Angola	LISC 8678
41	*Brachystegia taxifolia* Harms	−11.477	27.662	Boom A. (2016)	DRC	BRLU 24
42	*Brachystegia taxifolia* Harms	−11.533	27.463	Boom A. (2016)	DRC	BRLU 46
43	*Brachystegia taxifolia* Harms	−12.019	27.784	Duvigneaud P.	DRC	BRLU 3614 br2
44	*Brachystegia torrei* Hoyle	−15.587	39.614	Torre A.R., Paiva J. (1964)	Mozambique	LISC 11521
45	*Brachystegia wangermeeana* De Wild.	−10.693	23.182	Plancke J. (1958)	DRC	BRLU 154/2025
46	*Julbernardia paniculata* (Benth.) Troupin	−11.432	27.469	Boom A. (2016)	DRC	BRLU 51

KX673213). Final annotation was realized with GeSeq 1.71 (Tillich et al., 2017), graphically represented with OGDRAW 1.3 (Greiner et al., 2019; see Figure S1.1 in Supporting Information), and deposited in Genbank (accession number MW272922).

Following the workflow of Migliore et al. (2019), reads from the different low-coverage genomic libraries were mapped on the *Brachystegia* reference plastome using the Burrows-Wheeler Aligner BWA mem 0.7.12 (Li & Durbin, 2009). Only one inverted repeat (IR) was retained to facilitate the mapping and to avoid replicating non-independent sequence polymorphisms due to gene conversion between IRs. The aligned reads were converted to a mpileup file using Samtools 1.9 (Li et al., 2009) for consensus calling (i.e. calling genotype for each position for each individual) with Varscan 2.3.7 (Koboldt et al., 2012). The final dataset is a multi-fasta aligned matrix (available on Dryad: https://doi.org/10.5061/dryad.r4xgxd2b1), after excluding missing site positions, indels, and positions where heterozygosity was detected, in order to avoid nuclear copies of plastid regions (NUPTS) and heteroplasmy (Scarcelli et al., 2016).

2.4 | Phylogenetic inference

The chloroplast gene tree was inferred using both Maximum Likelihood (ML) and Bayesian Inference (BI) methods. The ML analysis was realized with RAxML-NG 0.9.0 (Kozlov et al., 2019), using the following parameters: 20 starting trees (10 random and 10 parsimony trees), a GTR+G model, and 1,000 bootstrap replicates. For the BI approach, we used MrBayes 3.2.6 (Ronquist et al., 2012) with the GTR+I+G model of substitution according to Jmodeltest2 (Darriba et al., 2012). Two runs of four chains each (i.e. one cold chain and three heated chains per run) were performed for 20,000,000 generations, sampling every 1,000 trees. The 50% majority-rule consensus tree was generated, after discarding 25% of the sampled trees as burnin. Runs converged as the average standard deviation of split frequencies dropped down to 0.002 after 5,000,000 generations (i.e. the burnin). After checking convergence diagnostic statistics (i.e. ESS and PSRF; Table S1.1), ML and BI trees were plotted using FigTree 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

To assess whether the plastid phylogeny was consistent with species delimitation and/or geographical regions, we generated inter-individual distance matrices using R (R Development Core Team, 2019) representing (a) phylogenetic distances (nucleotide distances between plastomes, computed using the R package 'ape'; Paradis & Schliep, 2019), (b) taxonomic distances (value of 0 between conspecific individuals, 1 between species) and (c) geographical distances (shortest distances along the earth surface computed by the R package 'geosphere'; Hijmans, 2019). We then tested the correlation between these matrices by Mantel tests using the R package 'vegan' (Oksanen et al., 2019). Correlation tests were performed on 42 *Brachystegia* individuals, as information on latitude and longitude coordinates were missing for three specimens (Table 1).

2.5 | Molecular dating

Calibrating a phylogeny remains challenging because it is subject to different sources of bias (e.g. fossils taphonomy and anchoring), as discussed for Detarioideae (Bruneau et al., 2008; de la Estrella et al., 2017; Koenen et al., 2019). Here, we performed a two-step dating approach, using BEAST 1.8.4 (Drummond et al., 2012): a large taxon sampling with multiple calibration points and data from three pastid genes was first used to estimate the divergence between *Brachystegia* and *Julbernardia*, which provided a secondary calibration point for dating the *Brachystegia* phylogeny based on aligned plastomes.

In the first step, we maximized the taxonomic coverage within Fabaceae, based on the alignment of Bruneau et al. (2008) for three plastid sequences (*mat*K, *trn*K and *trn*L). As detailed in Tosso et al. (2018), we retained 251 Fabaceae (including three *Brachystegia* samples) and eight outgroup taxa (i.e. species of the Quillajaceae, Polygalaceae and Surianaceae families). We used four fossil calibrations and one calibration of the crown age of Fabaceae derived from Koenen et al. (2019), as detailed in the Supporting Information (Method S1.1). According to Jmodeltest2 (Darriba et al., 2012), the substitution models GTR+G, GTR+G and HKY+G were applied to *mat*K, *trn*K and *trn*L gene partitions respectively. BEAST was run using as tree model, either the Yule process or the coalescent process of constant population size, and as clock model, either the strict clock or a relaxed clock with uncorrelated lognormal distribution. We selected the best models according to their marginal likelihoods using Bayes factors, as detailed in Supporting Information (Table S1.2). For each combination of tree and clock models, we launched two independent runs (100 million of generations, sampling 10,000 trees per run). Resulting log and tree files were combined using LogCombiner 1.8.4, removing 10% of the trees as burnin. Combined log files were examined with Tracer 1.7.1 (Rambaut et al., 2018) to check the posterior parameters, the effective sample sizes (ESS), and the convergence between runs. Combined trees were analysed using TreeAnnotator 1.8.4, to obtain the final maximum clade credibility tree and the posterior distribution of the time to the most recent common ancestor (TMRCA) between *Brachystegia* and *Julbernardia*.

In the second step, we maximized the number of characters, focusing on our 46 *Brachystegia* and *Julbernardia* aligned plastome sequences to construct a phylogenetic tree which was time-calibrated by the *Brachystegia-Julbernardia* TMRCA estimated in the first step. We applied the GTR+I+G substitution model, a coalescent tree prior (constant population size) and an uncorrelated lognormal relaxed clock model (Table S1.2, Supporting Information). Following the same procedure as previously described, all the BEAST runs were launched on the CIPRES gateway servers (Miller et al., 2010). The final chronogram was edited using FigTree 1.4.4.

In parallel, to test the robustness of our divergence time approach, an additional BEAST analysis was performed using a one-step calibration approach based on 24 taxa including more plastid markers (45 genes, 45,567 sites), as detailed in Supporting Information (Method S1.2).

3 | RESULTS

3.1 | Plastome data

After filtering, we obtained a mean of 1,269,221 good quality paired-end reads per library (*SD* = 663,400). The *B. bakeriana* plastome obtained by de novo assembly had a length of 159,544 bp (Small Single Copy: 19,672 bp; Long Single Copy: 87,859 bp; Inverted Repeat: 26,007 bp; Figure S1.1), with a mean depth coverage of 88 x. Removing one inverted repeat region, the reference plastid sequence used for mapping the other samples reached 133,537 bp in length. On average 3.3% (*SD* = 1.2%) of trimmed reads were mapped on the reference (mean number of reads = 89,079, *SD* = 62,180). This corresponds to a mean depth coverage of 56 x (standard deviation = 39). After removing position from the alignment containing missing data, indels and apparent heterozygotes (possibly due to NUPTs), it reached a length of 100,400 bp, corresponding to c. 75% of the original alignment. The final alignment contained 519

phylogenetically informative sites, for a total of 1,768 variable sites. Excluding the outgroup *Julbernardia*, the number of phylogenetically informative sites dropped down to 511, for a total of 1,160 variable sites.

3.2 | Phylogenetic relationships

Both BI and ML tree topologies were globally congruent (Figure 1, Figure S1.2, Supporting Information). Main nodes were well supported by bootstrap values (ML tree: ≥88) and posterior probabilities (BI tree: ≥0.96), except in the MW-western clade (see below) where RAxML bootstrap values ranged between 62 and 72 while BI posterior probabilities remained high (≥0.96). Four polytomies in the MrBayes tree were observed in terminal branches, in which relationships between haplotypes were weakly supported in the RAxML tree (ML tree: ≤34).

The nucleotide distances between *Brachystegia* samples were weakly correlated with taxonomical distances (r = 0.138, Mantel test, p-value = 0.001) but highly correlated with geographical distances (r = 0.747, Mantel test, p-value = 0.001). Accordingly, of the 15 species represented by multiple samples, only three with geographically adjacent specimens (*B. eurycoma*, *B. leonensis* and *B. taxifolia*) appeared monophyletic (Figure 1, Figure S1.2). *B. kennedyi* appeared also monophyletic in the ML topology, but with low support (bootstrap value = 34).

The first divergence between plastid lineages separated a rain forest clade (RF) and a clade including all samples and species from miombo plus one *B. laurentii* sample from Gabonese rain forest (miombo woodland *sensu lato* or MW *s.l.* clade) (Figures 1–3, Figure S1.2). The MW *s.l.* clade contained additionally an early branching sample of *B. bussei* from miombo (specimen Burtt 4736 [BR]). Remaining lineages formed a MW *sensu stricto* (MW *s.s.*) clade subdivided into three main parapatric subclades: an East African clade (Tanzania to Mozambique), a Central clade (Zambia to D. R. Congo) and a Western clade (D. R. Congo to Angola); the two latter were sister clades with overlapping distributions in the eastern part of the Upper Katanga (D. R. Congo) region (Figures 1–3). Within the East African clade, sister haplotypes were also geographically grouped, forming Eastern Tanganyika, Central Tanzania and Tanzania–Mozambique subclades. A similar pattern emerged in the RF clade which can be subdivided into three parapatric subclades centred on Upper Guinea, Southwest Nigeria and Southeast Nigeria-Cameroon (Figures 1–3). Accordingly, within each major clade (RF, MW *s.l.* and MW *s.s.*), nucleotide distances between individuals were still significantly correlated with geographical distances (Mantel tests: r = 0.546 in RF, 0.367 in MW *s.l.*, 0.449 in MW *s.s.*, p-values < 0.005) while they were less significantly correlated with taxonomic distances (Mantel tests: r = 0.341 in RF, 0.077 in MW *s.l.*, 0.159 in MW *s.s.*, p-values = 0.027, 0.017 and 0.002 respectively). Interestingly, within miombo subclades, the mean nucleotide distance, that is, mean proportion of different sites between pairs of sequences, increased from west to east (Western = 2.0×10^{-4}; Central = 4.2×10^{-4}; Eastern = 6.1×10^{-4}).

3.3 | Timing of divergence

The divergence time estimated between *Brachystegia* and *Julbernardia* was relatively congruent and overlapping: around

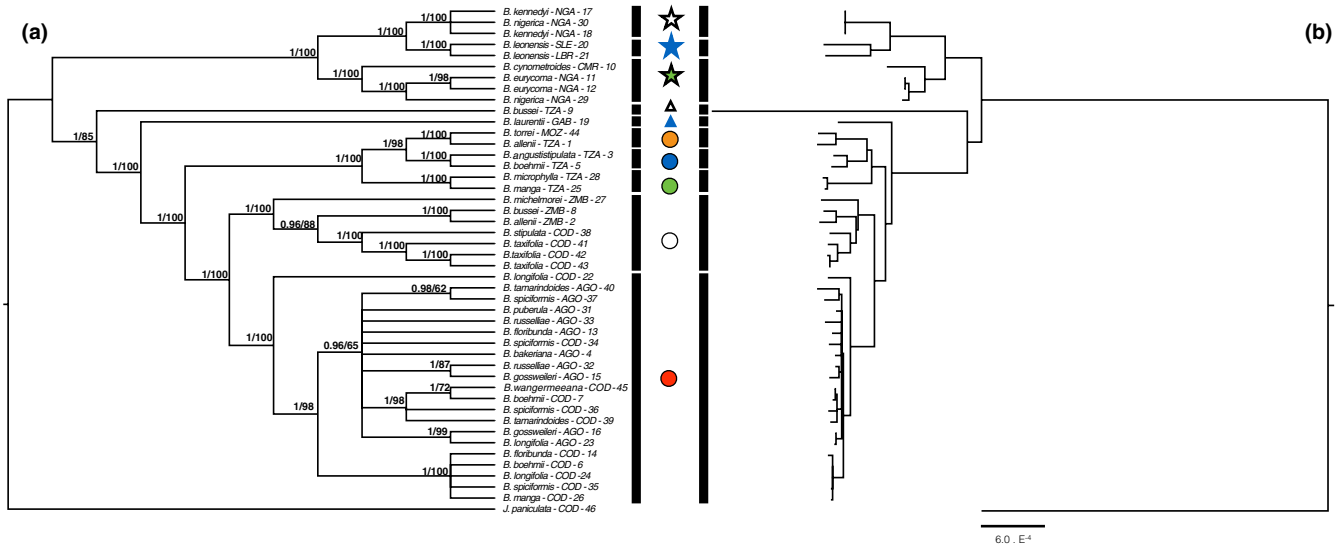

FIGURE 1 Cladogram (a) and 50% majority-rule consensus tree (b) of *Brachystegia* plastomes obtained using the Bayesian method implemented in MrBayes. Both trees were rooted using a sample of *Julbernardia paniculata*. Tip labels indicate the species name, the ISO code for the origin country, and the specimen ID (Table 1). Clades supports in (a) are provided as Bayesian posterior probabilities (left) and corresponding bootstrap support of the Maximum Likelihood phylogeny performed using RAxML-NG (right). The different clades and their corresponding symbols and colours are indicated between the two topologies, as shown in Figures 2 and 3 [Colour figure can be viewed at wileyonlinelibrary.com]

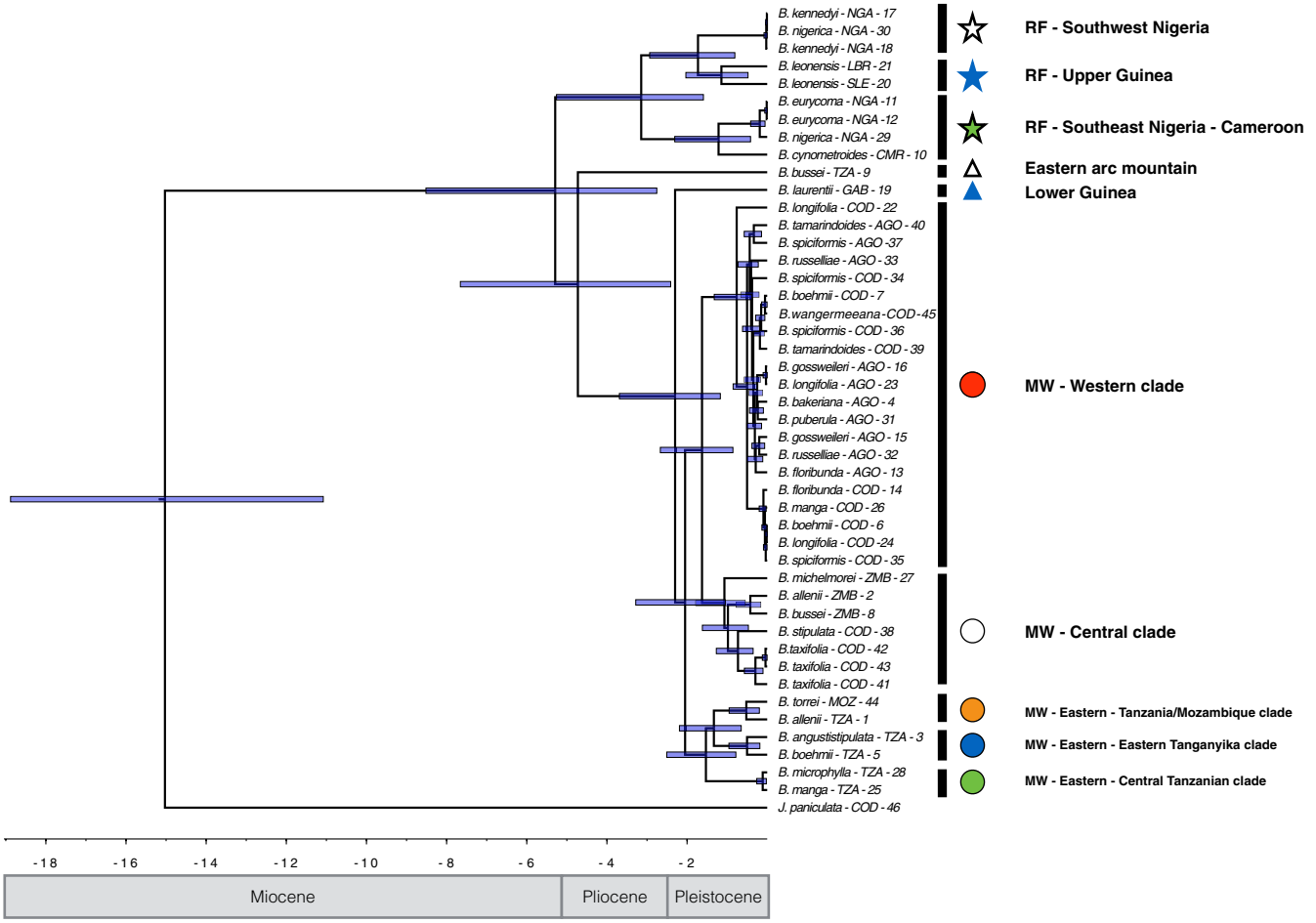

FIGURE 2 Chronogram of the plastid diversification of 45 *Brachystegia* samples and one *Julbernardia* outgroup, according to BEAST analysis (maximum clade credibility tree). Time units are in million years. Node bars indicate the 95% highest posterior density (HPD) interval. Tip labels indicate the species name, the ISO code for the origin country, and the specimen ID (Table 1). Clades and their corresponding coloured symbols, as used in Figure 3, are indicated on the right. RF and MW refer to the rain forest and the Miombo woodland *sensu stricto* clades, respectively (see Figure 3) [Colour figure can be viewed at wileyonlinelibrary.com]

15.03 Ma (95% HPD = 11.08–18.88), using three plastid sequences from 259 Fabaceae plus outgroup taxa (Figure S1.3, Supporting Information), and around 11.96 Ma (95% HPD = 8.36–15.95) according to the one-step approach using 24 taxa and 45 plastid markers (Table S1.3, Figure S1.4, Supporting Information). Although the one-step molecular dating approach inferred a younger divergence between *Brachystegia* and *Julbernardia*, it suggested an older TMRCA of *Brachystegia* by c. 1.7 Ma (7.03 Ma, 95% HPD = 4.75–9.69).

Considering the two-step dating approach, the RF and MW *s.l.* clades diverged 5.29 Ma (95% HPD = 2.76–8.52, Figure 2), while the TMRCA of the three miombo subclades was 2.05 Ma (95% HPD = 1.17–3.69, Figure 2). The TMRCA of samples from each of these subclades increased from west to east (Figure 2): 0.76 Ma (95% HPD = 0.38–1.32) for the Western clade, 1.07 Ma (95% HPD = 0.55–1.79) for the Central clade and 1.53 Ma (95% HPD = 0.78–2.51) for the East African clade. The TMRCA of the RF clade was older: 3.93 Ma (95% HPD = 1.59–5.26). These divergence times estimates were similar to the ones obtained using the one-step dating approach, also inferring a Plio-Pleistocene origin for the current lineages of the miombo *s.s.* clade (2.87 Ma, 95% HPD = 1.58–4.51), and the older age of the RF clade (3.63 Ma, 95% HPD = 1.83–5.81).

4 | DISCUSSION

4.1 | Introgression and plastid phylogeny

One of the main phylogenetic patterns detected in *Brachystegia* is that most species do not appear monophyletic in the plastid phylogenetic tree, rejecting our first hypothesis (H1) assuming well-separated and monophyletic species. Hence, plastid DNA is not appropriate for taxonomic delineation in this genus. This contrasts with the patterns observed in the African trees of genera *Guibourtia* (Tosso et al., 2018) and *Entandrophragma* (Monthe et al., 2019) where nearly all species appeared monophyletic. Incorrect species identification should not be at the origin of this pattern because ongoing work shows that most species appear monophyletic using nuclear markers (A. F. Boom, unpublished results). The absence

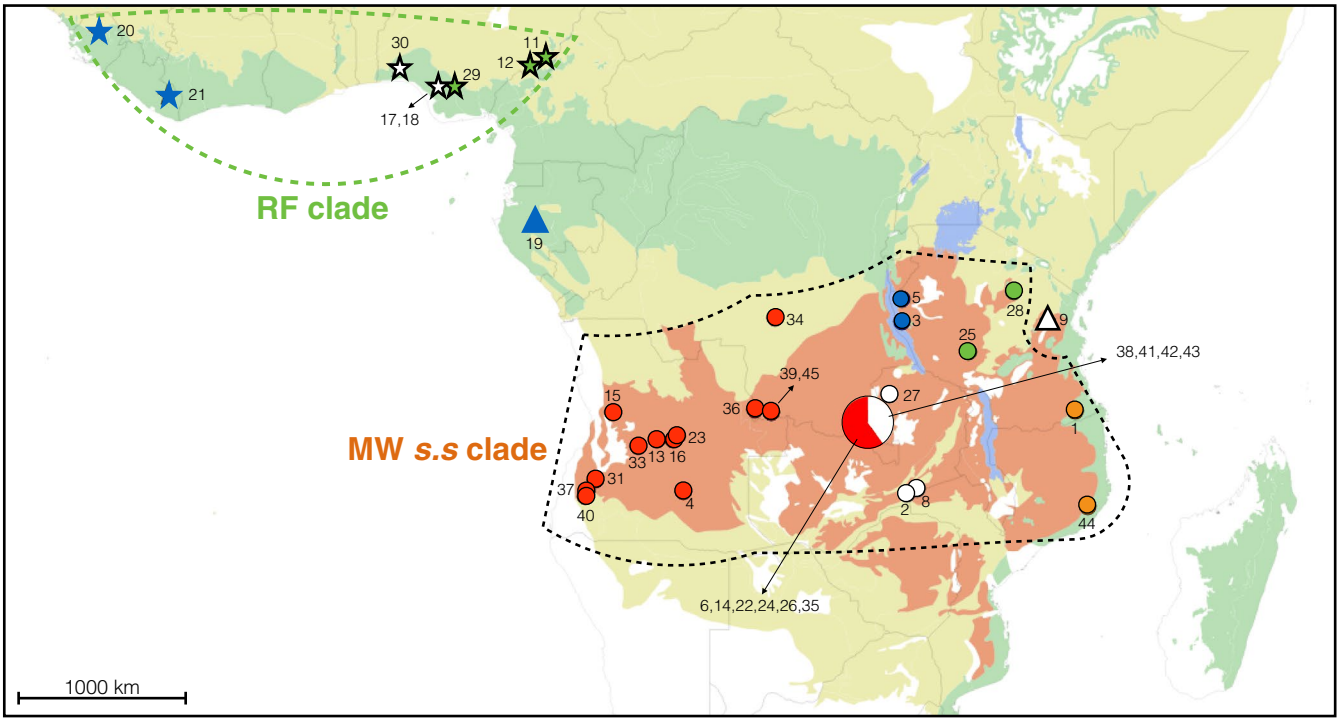

FIGURE 3 Spatial distribution of plastid lineages recovered in 42 *Brachystegia* trees sampled across Africa. Background colours indicate biomes following Olson et al. (2001): green for the tropical rain forest, red for miombo woodlands, yellow for other types of tropical and subtropical grasslands, savannahs and shrublands. The distribution of the rain forest clade (RF, stars, $n = 8$) and the miombo woodlands *sensu stricto* clade (MW *s.s.*, circles, $n = 32$) are delineated by dotted lines, while triangles show two haplotypes that do not fall in these clades and belong to *B. bussei* (white) and *B. laurentii* (blue). Different colours of a symbol indicate subclades found within each major clade, and numbers refer to specimen IDs (Table 1, Figure 1). The MW *s.s.* clade is subdivided into Western (red), Central (white) and East-African (blue, green and orange) subclades [Colour figure can be viewed at wileyonlinelibrary.com]

of monophyly could result from incomplete lineage sorting (ILS) if effective population sizes are large and/or speciation too recent, as assumed under our second hypothesis (H2). This situation could be expected for dominant species with large populations and wide distribution ranges in recent biomes (e.g. Cerrado savanna tree species, Pennington & Lavin, 2016), which might be valid for some *Brachystegia* species of the miombo. However, when shared lineages result from ILS, we do not expect a correlation between phylogenetic and geographical distances when we consider pairs of samples from distinct species (e.g. Muir & Schlötterer, 2004). As revealed by ML/BI phylogenies and Mantel tests, *Brachystegia* plastid diversity is much better explained by geography than by taxonomy (Figures 1–3), so that H2 can be rejected as well. This pattern is not uncommon in plants and has been reported for several genera as *Quercus* (Fagaceae), *Fraxinus* (Oleaceae), *Eucalyptus* (Myrtaceae), etc. for which it was mainly explained by hybridization and cytoplasmic introgression (Heuertz et al., 2006; Jackson et al., 1999; Petit et al., 2002; Pham et al., 2017). Hence, the phylogeographical pattern found in *Brachystegia* clearly supports our third hypothesis (H3) assuming widespread cytoplasmic introgression between species, leading to chloroplast captures, whereby distinct species tend to share locally the same plastid lineages. This phenomenon has been particularly evidenced for species with much higher pollen than seed dispersal abilities (Petit & Excoffier, 2009). Local trees are invaded by swamping pollen from other related species and through hybridization and subsequent backcrosses, plastid genomes are transferred from one species to another, where species are defined by their nuclear genome (Petit et al., 2003; Potts & Reid, 1988). In most angiosperms, the plastid genome is transmitted maternally and hence depends on seed dispersal, which is often less extensive than pollen dispersal, the latter largely contributing to the dispersal of the nuclear genome. Therefore, the plastid diversity is relatively static in space. Plant species prone to hybridization, where chloroplasts are maternally inherited and where pollen is better dispersed than seeds will therefore exhibit a topology in which the plastid diversity is to some degree species independent, but reflects geographical patterns.

A large difference in pollen and seed dispersal abilities is very likely in *Brachystegia* species. Canopy trees in miombo are known to be pollinated by bees (Smith, 1957) and seeds of legume trees are dispersed through explosive pods (Strang, 1966). Measurement of seed dispersal distances for *B. spiciformis* ranges from 6 to 20 m (Ernst, 1988; Malaisse, 1978). By contrast, bees can disperse pollen over several hundred metres to a few kilometres in tropical ecosystems (e.g. Jha & Dick, 2010). Parentage analyses would be necessary to better assess seed and pollen dispersal abilities because habitat, breeding system and pollination play a major role (e.g. Hardy

et al., 2019; Jha & Dick, 2010; Monthe et al., 2017), aspects that remains to characterize.

Several hybrids between *Brachystegia* miombo species have been described based on morphological and field evidence (White, 1962). Field observations (Lawton, 1962) have also reported two different types of *Brachystegia* stands in woodlands: pure stands with predominating distinct species and 'admixed' stands in which hybrids tend to occur more frequently. This supports the hypothesis of a dynamic system, corresponding to invasion from alien pollen and/or secondary contact of species originating from different miombo patches that were still disconnected recently. Several palaeoecological records also showed that the current contiguous miombo belt experimented contractions and expansions during the late Pleistocene in response to past climate changes (Roche, 1991). Hence, detailed studies of introgression patterns between co-occurring *Brachystegia* species at a local scale should be undertaken to test our hypothesis.

4.2 | Origin of *Brachystegia* lineages and biome shifts

Plastid sequences of *Brachystegia* and *Julbernardia* diverged during the Miocene (8–16 Ma and 11–19 Ma, depending of the method), and current lineages of *Brachystegia* diverged during the late Miocene–Pliocene (TMRCA estimated from 2.8 to 8.6 Ma). *Brachystegia* was supposed older according to pollen data because *Peregrinipollis nigericus* (Clarke, 1966), a palynomorph exhibiting morphological affinities with modern *Brachystegia* pollen (Clarke & Frederiksen, 1968), is documented up to the late Eocene (Kaska, 1989; Morley, 2000). Therefore, the dated phylogeny suggests that *P. nigericus* and *Brachystegia* spp. are less related than assumed before.

Brachystegia plastomes do not track species delineation, preventing us to infer speciation processes and to reconstruct the ancestral biome of the most recent common ancestor of *Brachystegia* species, so that the direction of biome shift (H5) cannot be tested. Consequently, a comprehensive history of ancestral biomes and species diversification is still unresolved and must be based on nuclear markers. However, the plastid topology delineated two major clades, geographically and ecologically differentiated, suggesting a single biome shift, and supporting the hypothesis that the ecological niche tends to be fairly conserved (H4). The divergence between the rain forest and miombo clades could be linked to adaptive diversification during a period marked by the expansion of C4 flammable ecosystem in Africa that started at the end of the Miocene, potentially supporting H6. However, the exact evolutionary relationship between Guineo-Congolian rain forest and woodland species remains hypothetical here for two reasons. First, the successfully sequenced rain forest samples mostly came from the Upper-Guinea bioregion and the only specimen from southern Central African rain forest (specimen Wieringa 4529 [BR]) is phylogenetically close to the MW *s.s.* lineages. Second, the MW *s.l.* contains an early-branching specimen (specimen Burtt 4736 [BR]) from the Turiani and Nguru mountains area of the Eastern arc system, known to host numerous plants and vertebrates restricted to forested habitats (Burgess et al., 2007). This haplotype could, therefore, be explained either by remnant woodland lineage from the late Miocene–Pliocene that predates most of the actual woodland diversity, or by introgression from now-extinct forest species hosted in the Eastern arc mountains by species from the surrounding miombo. Nevertheless, the plastid phylogeny provides insights into the spatial and demographical evolution of most of the extant lineages of the miombo clade (MW *s.s.*) and the rain forest clade (RF).

4.3 | Miombo and rain forest lineages

The Western, the Central and the Eastern African miombo subclades diverged and evolved during the Plio-Pleistocene (TMRCA from 1 to 3.3 Ma). This period is characterized by the expansion of C4 flammable ecosystem, an alternation between arid and wet climates, and geomorphologic rearrangements (deMenocal, 1995; McDonough et al., 2015). This supports the hypothesis that the diversification of miombo *Brachystegia* species may be synchronous, not with the origin of C4 flammable ecosystem (c. 10 Ma, our hypothesis H6), but with their wide development during the Plio-Pleistocene (Cerling, 1992). Lake Tanganyika, lake Malawi and the Rukwa basin apparently constituted strong geographical barriers for seed dispersal across all the Pleistocene, since the Central and Eastern plastid clades do not occur in sympatry at large spatial scales. The role of these barriers during the Pleistocene has already been documented for several species of rodents strongly associated with miombo landscapes (e.g. Bryja et al., 2018; Mazoch et al., 2018). However, this remains surprising as the two subclades are nowadays forming contiguous wooded landscapes.

The dated phylogeny and the mean nucleotide distances within miombo subclades indicate an older origin of *Brachystegia* in Eastern woodland, followed by Central and Western miombo (Figure 2). This supports East Africa as a cradle of the most typical genus of miombo woodland, followed by a colonization of south-central Africa. Contrasting with the two other miombo subclades, haplotypes of the Western subclade are nested in a group centred on D. R. Congo with polytomy and/or low supported short branches (Figures 1 and 2 and Figure S1.2). This could indicate a recent colonization and/or expansion from D. R. Congo to Angola, during the last million years. Interestingly, Upper-Katanga (southeast part of D. R. Congo) seems to be a contact zone where haplotypes of the Western and Central subclades occur in sympatry. This seems to coincide with floristic observations that recognize the non-homogeneous nature of Upper-Katangan floras, with a Kwango-Angolean floristic sector in the west, and a Katangan-Zambian sector in the east (Duvigneaud, 1958; Werger & Coetzee, 1978). We can thus hypothesize that in addition to a westward expansion starting from East Africa, miombo woodlands have undergone one or several phases of historical fragmentation explaining the biogeographical and phylogeographical breaks observed today.

Concerning the rain forest clade of *Brachystegia* plastomes, a phylogeographical pattern is also emerging, through three subclades restricted to Upper Guinea, Southwest Nigeria, and Southeast Nigeria-Cameroon (Figures 1–3). These subclades could result from a fragmentation of the rain forest induced by Pleistocene climate fluctuations (Maley, 1996) or reflect isolation-by-distance, as suggested from the plastome phylogeographical patterns conducted on Guineo-Congolian rain forest taxa (Faye et al., 2016; Migliore et al., 2019). African rain forest species with limited dispersal ability (e.g. ballistic fruit), such as *Brachystegia*, exhibit thus spatial genetic patterns generally associated with the presence of putative glacial refugia (Sosef, 1994) or microrefugia (Leal, 2001), even if west–east environmental filtering, heterogeneous topography and north–south seasonal inversion effects could also explain part of those patterns (e.g. Dauby et al., 2014; Heuertz et al., 2014). Nevertheless, the increasing number of phylogenomic studies based on plastid markers appears promising to explore the dynamics of rain forest though time (e.g. Demenou et al., 2020).

5 | CONCLUSIONS

In the genus *Brachystegia*, the distribution of plastid lineages is much better explained by geography than by taxonomy, highlighting the prevalence of plastid introgression between species, especially in miombo woodlands. Therefore, the phylogeny of *Brachystegia* plastomes is informative to better understand the evolutionary history of miombo of which *Brachystegia* species constitute a major structural component. It suggests that miombo lineages diverged from rain forest lineages in the late Miocene–Pliocene, and expanded from East Africa to central and western southern Africa during the Plio-Pleistocene, in a context of increased aridity, expansion of C4 savanna and climatic instability, which might have caused phases of fragmentation of miombo woodlands. A denser sampling and a better characterization of the species tree using nuclear markers will be necessary to validate species delineation and further infer their evolutionary trajectories.

ACKNOWLEDGEMENTS

This study was financially supported by the Belgian 'Fonds pour la Formation à la Recherche dans l'Industrie et l'Agriculture' – 'Fonds National pour la Recherche Scientifique' (FRIA-FNRS PhD grant to A.F.B), and by the BRAIN-be BELSPO research program BR/132/A1/AFRIFORD (postdoctoral grant to J.M.). We would like to express our gratitude to the Faculté des sciences agronomiques de Lubumbashi (DRC), for the logistic support provided during the field collection. We thank all the curators and other persons who helped us from the following herbaria: Stephen Harris and Serena Marner (FHO), Maria Cristina Duarte and Maria M. Romeiras (LISC), Steven B. Janssens and Ann Bogaerts (BR), Tariq Stévart and Geoffrey Fadeur (BRLU). We are very grateful to people involved in field collections: Michel Hasson, Annie and Richard De Cauwer, Eric Lowele, and Michel Anastassiou. We also acknowledge Laurent Grumiau (ULB-EBE Molecular Biology platform, Belgium), and Latifa Karim (GIGA Liège, Belgium) for their technical help. Plant material collection in Democratic Republic of the Congo and export benefited from the permit 023/2016 delivered by the Université de Lubumbashi, Faculté des sciences agronomiques de Lubumbashi

DATA AVAILABILITY STATEMENT

Plastome of *Brachystegia allenii* (specimen White 2406 A) available in GenBank (accession number MW272920). Plastome of *B. augustistipulata* (specimen Jefford, Juniper & Newbould 2799) available in GenBank (accession number MW272923). Reference plastome of *B. bakeriana* (specimen Dechamps, Murta & da Silva 1327) available in GenBank (accession number MW272922). Plastome of *B. eurycoma* (specimen Chapman 156) available in GenBank (accession number MW272919). Plastome of *B. kennedyi* (specimen Miekle & Keay 581) available in GenBank (accession number MW272921). Plastome of *J. paniculata* (specimen Boom 51) available in GenBank (accession numbers MW272924 and MW272925). Final plastid alignment available from the Dryad data repository (https://doi.org/10.5061/dryad.r4xgxd2b1). Alignments for 45 plastid genes available from the Dryad data repository (https://doi.org/10.5061/dryad.r4xgxd2b1).

ORCID

Arthur F. Boom https://orcid.org/0000-0001-5724-2754
Jérémy Migliore https://orcid.org/0000-0002-7534-9667
Pierre Meerts https://orcid.org/0000-0003-4215-027X
Olivier J. Hardy https://orcid.org/0000-0003-2052-1527

REFERENCES

Bakker, F. T., Lei, D. I., Yu, J., Mohammadin, S., Wei, Z., van de Kerke, S., Gravendeel, B., Nieuwenhuis, M., Staats, M., Alquezar-Planas, D. E., & Holmer, R. (2016). Herbarium genomics: Plastome sequence assembly from a range of herbarium specimens using an Iterative Organelle Genome Assembly pipeline. *Biological Journal of the Linnean Society*, *117*, 33–43. https://doi.org/10.1111/bij.12642

Beerling, D. J., & Osborne, C. P. (2006). The origin of the savanna biome. *Global Change Biology*, *12*, 2023–2031. https://doi.org/10.1111/j.1365-2486.2006.01239.x

Bruneau, A., Mercure, M., Lewis, G. P., & Herendeen, P. S. (2008). Phylogenetic patterns and diversification in the caesalpinioid legumes. *Botany-Botanique*, *86*, 697–718. https://doi.org/10.1139/B08-058

Bryja, J., Konvičková, H., Bryjová, A., Mikula, O., Makundi, R., Chitaukali, W. N., & Šumbera, R. (2018). Differentiation underground: Range-wide multilocus genetic structure of the silvery mole-rat does not support current taxonomy based on mitochondrial sequences. *Mammalian Biology*, *93*, 82–92. https://doi.org/10.1016/j.mambio.2018.08.006

Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Menegon, M., Moyer, D. C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W. T., & Stuart, S. N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, *134*, 209–231. https://doi.org/10.1016/j.biocon.2006.08.015

Campbell, B., Frost, P., & Byron, N. (1996). Miombo woodlans and their use: Overview and key issues. In B. Campbell (Ed.), *The Miombo in transition: Woodlands and welfare in Africa* (pp. 1–10). Centre for International Forestry Research.

Cappellini, E., Gilbert, M. T. P., Geuna, F., Fiorentino, G., Hall, A., Thomas-Oates, J., Ashton, P. D., Ashford, D. A., Arthur, P., Campos, P. F., Kool, J., Willerslev, E., & Collins, M. J. (2010). A multidisciplinary study of archaeological grape seeds. *Naturwissenschaften*, *97*, 205–217. https://doi.org/10.1007/s00114-009-0629-3

Cerling, T. E. (1992). Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *97*, 241–247. https://doi.org/10.1016/0921-8181(92)90013-Z

Chikuni, A. C. (1998). *A taxonomic study of Brachystegia benth. (Caesalpinioideae-leguminosae)*. University of Oxford.

Clarke, R. T. (1966). *Peregrinipollis nigericus*, a new palynomorph from the Upper Tertiary of Nigeria. *Grana Palynologica*, *6*, 544–546. https://doi.org/10.1080/00173136609430040

Clarke, R. T., & Frederiksen, N. O. (1968). Some new sporomorphs from the Upper Tertiary of Nigeria. *Grana Palynologica*, *8*, 210–224. https://doi.org/10.1080/00173136809427466

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

Daru, B. H., van der Bank, M., & Davies, T. J. (2018). Unravelling the evolutionary origins of biogeographic assemblages. *Diversity and Distributions*, *24*, 313–324. https://doi.org/10.1111/ddi.12679

Dauby, G., Duminil, J., Heuertz, M., Koffi, G. K., Stévart, T., & Hardy, O. J. (2014). Congruent phylogeographical patterns of eight tree species in Atlantic Central Africa provide insights into the past dynamics of forest cover. *Molecular Ecology*, *23*, 2299–2312. https://doi.org/10.1111/mec.12724

de la Estrella, M., Forest, F., Klitgård, B., Lewis, G. P., Mackinder, B. A., de Queiroz, L. P., Wieringa, J. J., & Bruneau, A. (2018). A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. *Scientific Reports*, *8*, 6884. https://doi.org/10.1038/s41598-018-24687-3

de la Estrella, M., Forest, F., Wieringa, J. J., Fougère-Danezan, M., & Bruneau, A. (2017). Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. *New Phytologist*, *214*, 1722–1735. https://doi.org/10.1111/nph.14523

deMenocal, P. B. (1995). Plio-Pleistocene African Climate. *Science*, *270*, 53–59. https://doi.org/10.1126/science.270.5233.53

Demenou, B. B., Migliore, J., Heuertz, M., Monthe, F. K., Ojeda, D. I., Wieringa, J. J., Dauby, G., Albreht, L., Boom, A., & Hardy, O. J. (2020). Plastome phylogeography in two African rain forest legume trees reveals that Dahomey Gap populations originate from the Cameroon volcanic line. *Molecular Phylogenetics and Evolution*, *150*, 106854. https://doi.org/10.1016/j.ympev.2020.106854

Donkpegan, A. S. L., Doucet, J.-L., Migliore, J., Duminil, J., Dainou, K., Piñeiro, R., Wieringa, J. J., Champluvier, D., & Hardy, O. J. (2017). Evolution in African tropical trees displaying ploidy-habitat association: The genus *Afzelia* (Leguminosae). *Molecular Phylogenetics and Evolution*, *107*, 270–281. https://doi.org/10.1016/j.ympev.2016.11.004

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Duvigneaud, P. (1958). Etudes sur la végétation du Katanga et de ses sols métallifères. *Bulletin de la Société Royale de Botanique de Belgique*, *90*, 127–286.

Ernst, W. H. O. (1988). Seed and seedling ecology of *Brachystegia spiciformis*, a predominant tree component in miombo woodlands in South Central Africa. *Forest Ecology and Management*, *25*, 195–210. https://doi.org/10.1016/0378-1127(88)90087-4

Faye, A., Deblauwe, V., Mariac, C., Richard, D., Sonké, B., Vigouroux, Y., & Couvreur, T. L. P. (2016). Phylogeography of the genus Podococcus (Palmae/Arecaceae) in Central African rain forests: Climate stability predicts unique genetic diversity. *Molecular Phylogenetics and Evolution*, *105*, 126–138. https://doi.org/10.1016/j.ympev.2016.08.005

Fayolle, A., Swaine, M. D., Aleman, J., Azihou, A. F., Bauman, D., te Beest, M., & Woollen, E. (2019). A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas. *Journal of Biogeography*, *46*, 454–465. https://doi.org/10.1111/jbi.13475

Frost, P. (1996). The ecology of miombo woodlands. In B. Campbell (Ed.), *The Miombo in transition: Woodlands and welfare in Africa* (pp. 11–57). Centre for International Forestry Research.

Furley, P. A., Rees, R. M., Ryan, C. M., & Saiz, G. (2008). Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe. *Progress in Physical Geography: Earth and Environment*, *32*, 611–634. https://doi.org/10.1177/0309133308101383

Greiner, S., Lehwark, P., & Bock, R. (2019). OrganellarGenomeDRAW (OGDRAW) version 1.3.1: Expanded toolkit for the graphical visualization of organellar genomes. *Nucleic Acids Research*, *47*, W59–W64. https://doi.org/10.1093/nar/gkz238

Hardy, O. J., Delaide, B., Hainaut, H., Gillet, J., Gillet, P., Kaymak, E., & Doucet, J. (2019). Seed and pollen dispersal distances in two African legume timber trees and their reproductive potential under selective logging. *Molecular Ecology*, *28*, 3119–3134. https://doi.org/10.1111/mec.15138

Heuertz, M., Carnevale, S., Fineschi, S., Sebastiani, F., Hausman, J. F., Paule, L., & Vendramin, G. G. (2006). Chloroplast DNA phylogeography of European ashes, *Fraxinus* sp. (Oleaceae): Roles of hybridization and life history traits. *Molecular Ecology*, *15*, 2131–2140. https://doi.org/10.1111/j.1365-294X.2006.02897.x

Heuertz, M., Duminil, J., Dauby, G., Savolainen, V., & Hardy, O. J. (2014). Comparative phylogeography in rainforest trees from Lower Guinea, Africa. *PLoS One*, *9*, e84307. https://doi.org/10.1371/journal.pone.0084307

Hijmans, R. J. (2019). *geosphere: Spherical Trigonometry*. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Hollingsworth, P. M., Li, D.-Z., van der Bank, M., & Twyford, A. D. (2016). Telling plant species apart with DNA: From barcodes to genomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150338. https://doi.org/10.1098/rstb.2015.0338

Jackson, H. D., Steane, D. A., Potts, B. M. P., & Vaillancourt, R. E. (1999). Chloroplast DNA evidence for reticulate evolution in *Eucalyptus* (Myrtaceae). *Molecular Ecology*, *8*, 739–751. https://doi.org/10.1046/j.1365-294X.1999.00614.x

Jacobs, B. F., & Herendeen, P. S. (2004). Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *213*, 115–123. https://doi.org/10.1016/S0031-0182(04)00368-2

Jha, S., & Dick, C. W. (2010). Native bees mediate long-distance pollen dispersal in a shade coffee landscape mosaic. *Proceedings of the National Academy of Sciences*, *107*, 13760–13764. https://doi.org/10.1073/pnas.1002490107

Jin, J.-J., Yu, W.-B., Yang, J.-B., Song, Y., dePamphilis, C. W., Yi, T.-S., & Li, D.-Z. (2019). GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. *bioRxiv*, 256479, https://doi.org/10.1101/256479

Kaska, H. V. (1989). A spore and pollen zonation of early cretaceous to tertiary nonmarine sediments of central Sudan. *Palynology*, *13*, 79–90. https://doi.org/10.1080/01916122.1989.9989356

Kissling, W. D., Eiserhardt, W. L., Baker, W. J., Borchsenius, F., Couvreur, T. L. P., Balslev, H., & Svenning, J.-C. (2012). Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences*, *109*, 7379–7384. https://doi.org/10.1073/pnas.1120467109

Koboldt, D. C., Zhang, Q., Larson, D. E., Shen, D., McLellan, M. D., Lin, L., Miller, C. A., Mardis, E. R., Ding, L., & Wilson, R. K. (2012). VarScan 2: Somatic mutation and copy number alteration discovery in cancer by exome sequencing. *Genome Research*, *22*, 568–576. https://doi.org/10.1101/gr.129684.111

Koenen, E. J. M., Ojeda, D. I., Steeves, R., Migliore, J., Bakker, F. T., Wieringa, J. J., Kidner, C., Hardy, O., Pennington, R. T., Herendeen, P. S., Bruneau, A. & Hughes, C. E. (2019). The origin and early evolution of the legumes are a complex paleopolyploid phylogenomic tangle closely associated with the Cretaceous-Paleogene (K-Pg) boundary, *bioRxiv*, 577957. https://doi.org/10.1101/577957

Kozlov, A. M., Darriba, D., Flouri, T., Morel, B., & Stamatakis, A. (2019). RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. *bioRxiv*, 447110. https://doi.org/10.1101/447110

Lawton, R. M. (1962). Palaeoecological and ecological studies in the Northern Province of Northern Rhodesia. *Kirkia*, *3*, 46–77.

Leal, M. E. (2001). Microrefugia, small scale ice age forest remnants. *Systematics and Geography of Plants*, *71*, 1073–1077. https://doi.org/10.2307/3668739

Lebrun, J.-P., & Stork, A. L. (2008). *Tropical African flowering plants: Ecology and distribution*, *Vol. 3: Mimosaceae – Fabaceae (incl. Derris)*. Conservatoire Botanique de Genève.

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*, *25*, 1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., & 1000 Genome Project Data Processing Subgroup (2009). The Sequence Alignment/Map format and SAMtools. *Bioinformatics*, *25*, 2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Linder, H. P. (2014). The evolution of African plant diversity. *Frontiers in Ecology and Evolution*, *2*, 38. https://doi.org/10.3389/fevo.2014.00038

Malaisse, F. (1978). The miombo ecosystem. *Tropical forest ecosystems* (pp. 589–606). UNESCO. https://wedocs.unep.org/handle/20.500.11822/30297

Maley, J. (1996). The African rain forest: Main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, *104*, 31–73. https://doi.org/10.1017/S0269727000006114

Mazoch, V., Mikula, O., Bryja, J., Konvičková, H., Russo, I.-R., Verheyen, E., & Šumbera, R. (2018). Phylogeography of a widespread sub-Saharan murid rodent *Aethomys chrysophilus*: The role of geographic barriers and paleoclimate in the Zambezian bioregion. *Mammalia*, *82*, 373–387. https://doi.org/10.1515/mammalia-2017-0001

McDonough, M. M., Šumbera, R., Mazoch, V., Ferguson, A. W., Phillips, C. D., & Bryja, J. (2015). Multilocus phylogeography of a widespread savanna-woodland-adapted rodent reveals the influence of Pleistocene geomorphology and climate change in Africa's Zambezi region. *Molecular Ecology*, *24*, 5248–5266. https://doi.org/10.1111/mec.13374

Migliore, J., Kaymak, E., Mariac, C., Couvreur, T. L. P., Lissambou, B., Piñeiro, R., & Hardy, O. J. (2019). Pre-Pleistocene origin of phylogeographical breaks in African rain forest trees: New insights from *Greenwayodendron* (Annonaceae) phylogenomics. *Journal of Biogeography*, *46*, 212–223. https://doi.org/10.1111/jbi.13476

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *2010 Gateway Computing Environments Workshop (GCE)*, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Monthe, F. K., Hardy, O. J., Doucet, J. L., Loo, J., & Duminil, J. (2017). Extensive seed and pollen dispersal and assortative mating in the rain forest tree Entandrophragma cylindricum (Meliaceae) inferred from indirect and direct analyses. *Molecular Ecology*, *26*(19), 5279–5291. https://doi.org/10.1111/mec.14241

Monthe, F. K., Migliore, J., Duminil, J., Bouka, G., Demenou, B. B., Doumenge, C., Blanc-Jolivet, C., Ekué, M. R. M., & Hardy, O. J. (2019). Phylogenetic relationships in two African Cedreloideae tree genera (Meliaceae) reveal multiple rain/dry forest transitions. *Perspectives in Plant Ecology, Evolution and Systematics*, *37*, 1–10. https://doi.org/10.1016/j.ppees.2019.01.002

Morley, R. J. (2000). *Origin and evolution of tropical rain forests*. John Wiley & Sons.

Morley, R. J., & Richards, K. (1993). Gramineae cuticle: A key indicator of Late Cenozoic climatic change in the Niger Delta. *Review of Palaeobotany and Palynology*, *77*, 119–127. https://doi.org/10.1016/0034-6667(93)90060-8

Muir, G., & Schlötterer, C. (2004). Evidence for shared ancestral polymorphism rather than recurrent gene flow at microsatellite loci differentiating two hybridizing oaks (*Quercus* spp.). *Molecular Ecology*, *14*, 549–561. https://doi.org/10.1111/j.1365-294X.2004.02418.x

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H., & Wagner, H. (2019) *vegan: Community Ecology Package*. R package version 2.5-5. https://CRAN.R-project.org/package=vegan

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N.I D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pennington, R. T., & Lavin, M. (2016). The contrasting nature of woody plant species in different neotropical forest biomes reflects differences in ecological stability. *New Phytologist*, *210*, 25–37. https://doi.org/10.1111/nph.13724

Pennington, R. T., Lehmann, C. E. R., & Rowland, L. M. (2018). Tropical savannas and dry forests. *Current Biology*, *28*, R541–R545. https://doi.org/10.1016/j.cub.2018.03.014

Pennington, R. T., Richardson, J. E., & Lavin, M. (2006). Insights into the historical construction of species-rich biomes from dated plant phylogenies, neutral ecological theory and phylogenetic community structure. *New Phytologist*, *172*, 605–616. https://doi.org/10.1111/j.1469-8137.2006.01902.x

Petit, R. J., Bodénès, C., Ducousso, A., Roussel, G., & Kremer, A. (2003). Hybridization as a mechanism of invasion in oaks: Research review. *New Phytologist*, *161*, 151–164. https://doi.org/10.1046/j.1469-8137.2003.00944.x

Petit, R. J., Csaikl, U. M., Bordács, S., Burg, K., Coart, E., Cottrell, J., van Dam, B., Deans, J. D., Dumolin-Lapègue, S., Fineschi, S., Finkeldey, R., Gillies, A., Glaz, I., Goicoechea, P. G., Jensen, J. S., König, A. O., Lowe, A. J., Madsen, S. F., Mátyás, G., … Kremer, A. (2002). Chloroplast DNA variation in European white oaks. *Forest Ecology and Management*, *156*, 5–26. https://doi.org/10.1016/S0378-1127(01)00645-4

Petit, R. J., & Excoffier, L. (2009). Gene flow and species delimitation. *Trends in Ecology and Evolution*, *24*, 386–393. https://doi.org/10.1016/j.tree.2009.02.011

Pham, K. K., Hipp, A. L., Manos, P. S., & Cronn, R. C. (2017). A time and a place for everything: Phylogenetic history and geography as joint predictors of oak plastome phylogeny. *Genome*, *60*, 720–732. https://doi.org/10.1139/gen-2016-0191

Polissar, P. J., Rose, C., Uno, K. T., Phelps, S. R., & deMenocal, P. (2019). Synchronous rise of African C4 ecosystems 10 million years ago in the absence of aridification. *Nature Geoscience*, *12*, 657–660. https://doi.org/10.1038/s41561-019-0399-2

Potts, B. M., & Reid, J. B. (1988). Hybridization as a dispersal mechanism. *Evolution*, *42*, 1245–1255. https://doi.org/10.2307/2409008

Prance, G. T. (2006). Tropical savannas and seasonally dry forests: An introduction. *Journal of Biogeography*, *33*, 385–386. https://doi.org/10.1111/j.1365-2699.2005.01471.x

R Development Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Radcliffe-Smith, A. (1993). Notes on African Euphorbiaceae XXIX: Uapaca. *Kew Bulletin*, *48*, 611–617. https://doi.org/10.2307/4118724

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics Using Tracer 1.7. *Systematic Biology*, *67*, 901–904. https://doi.org/10.1093/sysbio/syy032

Rieseberg, L. H., & Soltis, D. E. (1991). Phylogenetic consequences of cytoplasmic gene flow in plants. *Evolutionary Trends in Plants*, *5*, 65–84.

Roche, E. (1991). Evolution des paléoenvironnements en Afrique centrale et orientale au Pléistocène supérieur et à l'Holocène. Influences climatiques et anthropiques. *Bulletin de la Société Géographique de Liège*, *27*, 187–208.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542. https://doi.org/10.1093/sysbio/sys029

Savolainen, V., Cuénoud, P., Spichiger, R., Martinez, M. D. P., Crèvecoeur, M., & Manen, J.-F. (1995). The use of herbarium specimens in DNA phylogenetics: Evaluation and improvement. *Plant Systematics and Evolution*, *197*, 87–98. https://doi.org/10.1007/BF00984634

Scarcelli, N., Mariac, C., Couvreur, T. L. P., Faye, A., Richard, D., Sabot, F., Berthouly-Salazar, C., & Vigouroux, Y. (2016). Intra-individual polymorphism in chloroplasts from NGS data: Where does it come from and how to handle it? *Molecular Ecology Resources*, *16*, 434–445. https://doi.org/10.1111/1755-0998.12462

Schmitz, A. (1962). Les muhulu du Haut-Katanga méridional. *Bulletin du Jardin Botanique de l'état a Bruxelles*, *32*, 221–299. https://doi.org/10.2307/3667284

Simeone, M. C., Cardoni, S., Piredda, R., Imperatori, F., Avishai, M., Grimm, G. W., & Denk, T. (2018). Comparative systematics and phylogeography of *Quercus* Section *Cerris* in western Eurasia: Inferences from plastid and nuclear DNA variation. *PeerJ*, *6*, e5793. https://doi.org/10.7717/peerj.5793

Simon, M. F., & Pennington, T. (2012). Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences*, *173*, 711–723. https://doi.org/10.1086/665973

Smith, F. G. (1957). Bee botany in East Africa. *The East African Agricultural Journal*, *23*, 119–126. https://doi.org/10.1080/03670074.1957.11665132

Sosef, M. S. M. (1994). *Refuge Begonias: Taxonomy, phylogeny and historical biogeography of Begonia sect. Loasibegonia and sect. Scutobegonia in relation to glacial rain forest refuges in Africa*. Agricultural University.

Strang, R. M. (1966). The spread and establishment of *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin in the Rhodesian highveld. *The Commonwealth Forestry Review*, *45*, 253–256.

Tillich, M., Lehwark, P., Pellizzer, T., Ulbricht-Jones, E. S., Fischer, A., Bock, R., & Greiner, S. (2017). GeSeq – versatile and accurate annotation of organelle genomes. *Nucleic Acids Research*, *45*, W6–W11. https://doi.org/10.1093/nar/gkx391

Timberlake, J., Chidumayo, E., & Sawadogo, L. (2010). Distribution and characteristics of African dry forests and woodlands. In E. Chidumayo, & D. J. Gumbo (Eds.), *The dry forest and woodlands of Africa: Managing for products and services* (pp. 11–42). Earthscan London.

Tosso, F., Hardy, O. J., Doucet, J.-L., Daïnou, K., Kaymak, E., & Migliore, J. (2018). Evolution in the Amphi-Atlantic tropical genus *Guibourtia* (Fabaceae, Detarioideae), combining NGS phylogeny and morphology. *Molecular Phylogenetics and Evolution*, *120*, 83–93. https://doi.org/10.1016/j.ympev.2017.11.026

Trapnell, C. G. (1959). Ecological results of woodland and burning experiments in Northern Rhodesia. *Journal of Ecology*, *47*, 129–168. https://doi.org/10.2307/2257252

Veranso-Libalah, M. C., Kadereit, G., Stone, R. D., & Couvreur, T. L. P. (2018). Multiple shifts to open habitats in Melastomateae (Melastomataceae) congruent with the increase of African Neogene climatic aridity. *Journal of Biogeography*, *45*, 1420–1431. https://doi.org/10.1111/jbi.13210

Werger, M. J. A., & Coetzee, B. J. (1978). The Sudano-Zambezian region. In M. J. A. Werger (Ed.), *Biogeography and ecology of southern Africa* (pp. 301–462). Junk.

White, F. (1962). *Forest flora of Northern Rhodesia*. Oxford University Press.

White, F. (1986). *La végétation de l'Afrique: Mémoire accompagnant la carte de végétation de l'Afrique Unesco-AETFAT-UNSO*. ORSTOM; UNESCO.

Wick, R. R., Schultz, M. B., Zobel, J., & Holt, K. E. (2015). Bandage: Interactive visualization of de novo genome assemblies. *Bioinformatics*, *31*, 3350–3352. https://doi.org/10.1093/bioinformatics/btv383

BIOSKETCH

Arthur F. Boom research focuses on the origin and evolution of African flora using molecular and phylogenetic tools. This manuscript is part of his thesis work on the evolution and phylogenomics of the genus *Brachystegia*, conducted at the Université Libre de Bruxelles (ULB). A.F.B. also works on the use and development of metagenomic approaches in ecology (e.g. diet studies).

Author contributions: A.F.B., O.J.H. and P.M. planned the research questions. Herbarium material was collected by A.F.B., with the contribution of P.M. to field sampling. A.F.B., E.K. and J.M. performed laboratory work. A.F.B. and J.M. performed the analyses. A.F.B was responsible for the writing of the paper, with significant contributions from J.M., O.J.H. and P.M. All authors gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Boom AF, Migliore J, Kaymak E, Meerts P, Hardy OJ. Plastid introgression and evolution of African miombo woodlands: New insights from the plastome-based phylogeny of *Brachystegia* trees. *J Biogeogr.* 2021;48:933–946. https://doi.org/10.1111/jbi.14051