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Phylogenetic biome conservatism underlies the evolution of forest palaeoendemic legume trees in tropical Africa

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Biome conservatism is prevalent during the evolution of plant lineages. However, studies assessing biome lability, i.e. the capacity to shift biomes and its impact on tropical tree species diversification is currently limited. To address this, we analysed an endemic lineage of African tropical trees to investigate phylogenetic patterns of biome conservatism and lability and their impact on speciation and extinction rates. We reconstructed a time-calibrated phylogeny of the Berlinia clade (16 genera, 201 species) using 140 nuclear genes, 75% of its extant species and two fossil calibrations. We found the forest biome as the ancestral habitat and we inferred nine independent shifts from forest to savanna with no reversals. The forest biome is mostly conserved within the Berlinia clade, while the ability to shift to the savanna biome is randomly distributed across the group. We found five palaeoendemic genera that have persisted solely in the forest biome since the Oligocene. However, the ability to shift among biomes does not seem to influence speciation or extinction rates. Our results suggest that palaeoendemic and forest-restricted lineages are more susceptible to habitat alterations and climate change than lineages with biome lability, due perhaps to an innate limitation to adapt to new habitat types.

1. Introduction

Phylogenetic niche conservatism is the tendency of closely related species to retain similar ancestral bioclimatic affinities in comparison to more distant species [1], and it is considered a major determinant of global biodiversity patterns [2]. On a broader geographic scale, subtle variations among niches are captured into biomes. Biomes capture major vegetation types defined by climate, life form and ecophysiology and shifts among biome types are considered major transitions involving important adaptations [1]. Here, we chose the use of biome conservatism over niche conservatism considering the geographic scale of our analyses, the macroevolutionary time frame of our focal group and the methodology we used to characterize the forest and savanna biomes. Elucidating the distribution of biome conservatism and its lability (the propensity to evolve and transcend major ecological boundaries) through the evolutionary history of plant lineages can provide useful insights into their evolutionary potential under future climate change.

Understanding the distribution of biome lability among lineages is particularly relevant for tropical trees, which due to their long generation times, restricted distribution and habitat specificity might be more susceptible to changing climatic conditions. Previous studies at regional [3–5] and global levels [3,6–10] suggest that biome conservatism has been prevalent during angiosperm evolution, including in tropical forest tree lineages [11].

Understanding biome transitions is also particularly relevant in regions where major changes in biome types have occurred in the past over wide evolutionary time frames [12]. In Africa, the tropical rainforest biome has experienced an overall decline of area since its maximum extension in the early Eocene to the middle Miocene (55–11 Ma) [13]. This contraction has been proposed as one of the reasons for the depauperate species diversity of many tropical tree lineages in Africa (e.g. palms and some legume lineages) [14] compared with their counterparts in Asia and the Neotropical regions [15,16]. On the other hand, the overall reduction in rainforest areas in tropical Africa since the Eocene, coupled with the emergence of new available habitat types (such as the savanna biome), created opportunities for biome shifts and changes in diversification rates.

In spite of this, a recent analysis suggested that biome conservatism is prevalent in most (93%) speciation events in tropical African tree species at the supra-genus level [17]. Indeed, evidence shows that several arborescent forest taxa contracted and expanded their distribution range with the cycles of rainforest changes without shifting biomes [11,18,19]. Thus, despite the emergence of new biomes, most African tree lineages have maintained their ancestral biome across wide evolutionary time frames. It appears then that the capacity to shift between the forest and savanna biomes is unevenly distributed across clades [17]. This suggests that some lineages could be more susceptible to higher extinction rates when the availability of these biomes is altered. However, understanding the distribution of biome lability among lineages and the timing of their shifts requires robust time-calibrated phylogenetic reconstructions at the species level with good representation of extant taxa. In Africa, the Guineo-Congolian lowland rainforest has been identified as a region rich in plant palaeoendemism [20,21]. Palaeoendemic genera (taxa that diverged early within a particular clade and usually with a restricted distribution) have been previously suggested in the Berlinia clade (Leguminosae, subfamily Detarioideae) [22], a group of tropical tree legumes that diversified in the Guineo-Congolian region. Unlike many African forest tree taxa, the Berlinia clade seems to have experienced an increase in diversification rates since the Miocene [22]. The most recent analyses within this clade indicate different diversification patterns, where some lineages seem to have exploited the forest biome, while others were able to colonize new biomes, such as open grasslands and woodlands, that became available as the forest cover area reduced [22,23]. However, limited representation of the group in previous phylogenetic analyses has hindered the reconstruction of the distribution of biome lability and whether this capacity has led to higher speciation and/or extinction rates.

To understand more in depth the distribution of biome conservatism and lability, we reconstructed the phylogeny of all 16 genera of the Berlinia clade, including 75% of all extant species. We generated a time-calibrated phylogenetic tree using two fossils from the Miocene to investigate the position and the timing of biome shifts. Specifically, we aim to test the following hypotheses: (i) biome types show phylogenetic signal suggesting that some genera within the Berlinia clade have remained in their ancestral biomes despite the availability of new habitats during their evolutionary history; (ii) the capacity to shift biomes (i.e. biome lability) from forest to savanna is non-randomly distributed at the genus level within the Berlinia clade; (iii) lineages with the capacity to shift biomes show higher diversification rates compared with lineages that retain the ancestral forest biome; and (iv) lineages that retained their ancestral forest biome have higher extinction rates compared with lineages that adapted to the savanna biome.

2. Material and methods

(a) The study system

Here we studied the Berlinia clade, an endemic African group within the subfamily Detarioideae. The Berlinia clade consists of 16 genera, nine of which are composed of 10 or more species, totalling approximately 201 species [24]. We included all 16 genera, and 152 species, representing 75% of the extant species (electronic supplementary material, table S1). We used *Paramacrolobium coeruleum* as outgroup species in all our analyses.

(b) DNA extraction and target enrichment

DNA was extracted from 25 to 35 mg leaf material obtained from herbarium specimens or silica gel dried samples using a modified CTAB protocol [25] and cleaned using the QIAquick PCR Purification Kit (Qiagen, Venlo, The Netherlands). We prepared libraries using a modified version of the protocol reported in [26]. Hybrid enrichment was done using the Detarioideae v. 1 bait [23] on pools of 48 samples per reaction according to the MYbaits v. 2.3.1 protocol, with 23 h of hybridization, a high stringency post-hybridization wash, and a final amplification using 15 PCR cycles. The Detarioideae v. 1 bait [23] consists of 6565 probes (120 bp long overlapping baits) targeting 1021 exons from 289 genes. Paired-end sequencing (2 × 150 bp) was carried out on an Illumina NextSeq with reagent kit V2 at the GIGA platform (Liège, Belgium), assigning approximately 400 000 reads/sample. We recovered orthologues following a previously used pipeline [27], which was initially described in [23]. More details in the electronic supplementary material.

(c) Phylogenomic reconstruction with individual orthologues, concatenated and multispecies coalescent approaches

We did separate phylogenetic reconstructions on each orthologue (gene tree) and on the concatenated matrix (supermatrix) with maximum likelihood (ML) as implemented in RAxML v. 8.2.9 [28] using the GTRCAT model with -f a flags, 1000 bootstraps and default settings. We also carried out a ML analysis as implemented in IQ-TREE 1.6.1 [29] with ultrafast likelihood bootstrap with 1000 replicates. In addition, we carried out a Bayesian analysis using MrBayes 3.2.6 [30,31] on the concatenated matrix. For the Bayesian analyses, we applied four chains, two runs of 50 000 000 generations with the invgamma rate of variation and a sample frequency of 5000. The performance of the Bayesian analysis was assessed with Tracer 1.7 [32]. The species tree estimation was done under the coalescent model using the individual ML gene trees obtained with RAxML to infer a species tree with ASTRAL-II v. 5.5.7 [33]. Support was estimated using local posterior probability (LPP). We used FigTree [34] to visualize and edit the trees obtained from all the analyses.

(d) Climate niche modelling and categorization of biomes

The biomes of the 152 sequenced species in the Berlinia clade were derived from a larger dataset that includes biome occupancy for over 4000 tropical African species [17]. The dataset was constructed using georeferenced herbarium specimens extracted from the RAINBIO project [35] along with bioclimatic variables [36]. We used climatic ordination to assign each species to its respective climatic niche [37]. Hierarchical clustering based on niche similarity was then applied to group species, with the primary division reflecting the separation between species inhabiting forest and savanna biomes. The biome assignment was further corroborated with literature, descriptions from herbarium specimens and from our expertise of the distribution. Biomes were further corroborated with recent taxonomic revisions for all representatives in *Anthonotha* [38], *Englerodendron* [39], *Microberlinia* [40] and the monotypic genera *Icuria* [41], *Michelsonia* [40] and *Librevillea* [42,43] (electronic supplementary material, table S3).

(e) Selection of fossils and divergence time estimates

Given that previous age estimates of the Berlinia clade included a single fossil and a limited representation of extant species within its genera [23], we re-estimated the divergence times within the clade with two new fossils assigned to the Berlinia clade and constrained the maximum age of the clade with date estimates from two previous Leguminosae family-wide calibrations [44,45]. Here, we included fossils from leaves/lamina reported from Ethiopia from forest species of *Anthonotha shimaglae* and *Englerodendron mulugetanum* from the early Miocene dated at 21.7 Ma [46,47]. Both fossils share leaf macromorphological characteristics with other genera in the Berlinia clade, *Englerodendron, Berlinia* and *Isoberlinia*, including paripinnate compound leaves, symmetrical leaflets elliptic to falcate in shape, pulvinate petiolule, symmetry of the leaf base, secondary venation patterns and leaflet apex with a drip tip [46,47]. Leaflet traits in *A. shimaglae*, including entire-marginated, their venation, symmetry, acuminate apices and terete pulvinate petioles are only present in *Anthonotha* and *Englerodendron. Anthonotha shimaglae* also shares leaflet micromorphological features, such as trichome bases and periclinal papillae on the abaxial surface with some extant *Anthonotha* species, strongly indicating the assignment of this fossil within *Anthonotha* [46].

The fossil *E. mulugetanum* has unique leaf epidermal cuticle characteristics, such as sinuous anticlinal cell walls (omega shape) on both sides, which are not shared with other closely related genera, *Anthonotha, Berlinia* or *Isoberlinia* [47]. In addition, *E. mulugetanum* shares pollen features (striate sculpture) with *Berlinia, Anthonotha* and *Isoberlinia*, but not with *Oddoniodendron* (rugulate sculpture). An additional characteristic of the pollen, inconspicuous pori, is only shared with some extant *Englerodendron* species, justifying the assignment of this fossil to *Englerodendron* [47]. Given the shared leaf lamina and pollen characteristics of the two fossils with extant *Berlinia* and *Isoberlinia*, but different from *Oddoniodendron*, we used two strategies to constrain the age estimates of the Berlinia clade. In one conservative approach, we used their ages to constrain the clade containing *Anthonotha, Englerodendron, Berlinia* and *Isoberlinia* and another more restrictive one, using their ages to constrain only the clade including *Anthonotha* and *Englerodendron* (figure 1). We did not include a fossil assigned to *Aphanocalyx*, *A. singidaensis* (46 Ma) [48] given that the leaf traits from this fossil, such as the presence of a primary vein, sessile petiolule and eucamptodromous secondary venation, are shared with several extant genera from tribes Detarieae and Amherstieae [48]. It is thus most likely that *A. singidaensis* constitutes a stem member of either of these two tribes and does not represent a crown member of *Aphanocalyx*. Older age estimates have been recovered when *A. singidaensis* has been used to constrain the crown age of *Aphanocalyx* [49] or the Berlinia clade [22] compared with studies that used the age of *A. singidaensis* as a crown member of the tribe Amherstieae [44,50]. We also excluded pollen fossils of *Striatopollis catatumbus* and *Peregrinipollis nigericus* that have been assigned to genera within the Berlinia clade (e.g. *Brachystegia, Didelotia, Anthonotha, Berlinia, Isoberlinia*) [48,51–53]. These pollen fossils range in ages between 24 and 56 Ma and their assignment to extant genera is ambiguous, even when machine learning approaches were combined with training datasets of extant genera of tribe Amherstieae [54,55]. Despite the efficacy of ML approaches to assign pollen fossils to extant genera [54,55], the limited representation of extant genera from the Amherstieae tribe included in the training data set (16 out of 50 genera) limits the confidence of using pollen fossils to constrain crown ages of genera within the Berlinia clade. It is likely that most of these pollen fossils represent stem members of Amherstieae, rather than crown members of extant genera within the Berlinia clade. Future comparative analyses of pollen fossils of *Striatopollis* and *Peregrinipollis* with a wider representation of extant genera are required before we can use them to constrain nodes in the Berlinia clade. Finally, we used previous age estimates of the tribe Amherstieae obtained from broad dating calibrations across Leguminosae [44,45] to set a maximum age range of 42–52 Ma for the Berlinia clade (figure 1).

We identified a subset of 38 clock-like genes (root-to-tip variance) from the total genes recovered with the Detariodeae kit using the SortaDate pipeline [56]. These 38 clock-like genes also have enough level of total tree length (as a measure of sequence variation). We estimated divergence times with BEAST v. 2.7.7 [57] under a HYK substitution model with strict clock, coalescence constant-size and a speciation Yule process with a gamma distribution. We ran five independent runs of 200 million generations each, sampling trees and parameters every 10 000 generations, and a final burn-in of 20 million generations. Then, we used Tracer 1.7 [32] to assess convergence among the chains as well as to ensure that the effective sample size (ESS) value was above 200 in all parameters. We used FigTree [34] to generate the input tree used in the diversification analyses.

(f) Ancestral state reconstruction and biome shifts

We mapped the two biomes at the species level to reconstruct ancestral states within the Berlinia clade and to infer the number of biome shifts. Biomes and ancestral state reconstructions were analysed on the best RAxML tree recovered from the concatenated dataset. We ran the reconstructions using parsimony and likelihood methods as implemented in Mesquite v. 2.75 [58]. The number of inferred biome shifts from this analysis was later used to estimate the level of aggregation of biome lability (see below). We assessed the phylogenetic signal [59] for biomes (forest and savanna) using two approaches. First, we used the 'delta' function (https://github.com/mrborges23/delta_statistic?tab=readme-ov-file), which measures the degree of phylogenetic signal for a categorical trait. The obtained δ-value was then compared with random δ-values obtained from 100 random permutations of the tips in our phylogenetic tree. A low p-value (<0.05) meant that a given trait shows significant phylogenetic signal. Second, we used the R package caper [60] to compute the D metric based on the sum of sister-clade differences in the phylogeny [61], and run 1000 permutations to obtain the probability under a random (D = 1) phylogenetic structure. We used the best RAxML tree from the concatenated dataset and the tree from the BEAST calibration to run the two analyses.

Finally, we evaluated the level of aggregation of biome lability at the genus level (labile versus non-labile) using the mean phylogenetic distance between the number of instances where this trait evolved in the Berlinia clade using the tree we obtained from the RAxML concatenated analysis. Here, we considered a genus as labile if it contains both forest and savanna species. First, we converted the RAxML to an ultrametric tree using the chronos function in ape (lambda = 0). We then tested the null hypothesis that the instances of biome lability at the genus level (six nodes for the genera *Julbernardia, Bikinia, Aphanocalyx, Brachystegia, Berlinia* and *Isoberlinia*) in the Berlinia clade were aggregated compared with 1000 random set of nodes using a custom-made R script (available from Zenodo, DOI:10.5281/zenodo.20038126).

(g) Diversification rates in the forest and savanna lineages

(i) Time-dependent diversification

To assess the variation on diversification over time, we did a time-dependent diversification analysis as implemented in RPANDA [62]. We tested six models: (i) constant speciation rate (λcon) with no extinction (Yule null model), (ii) exponential variation of speciation rate (λexp) with no extinction, (iii) linear variation of speciation rate (λlin) with no extinction, (iv) constant speciation and extinction rates, (v) exponential speciation rates with a constant extinction rate, and (vi) linear speciation rates with a constant extinction rate [62]. The previous six models estimate current speciation and extinction rates and their rate variation over time up to the crown age. The diversification rates and major shifts were also evaluated using a Bayesian approach with the reversible MCMC method as implemented in BAMM v. 2.5.0 [63,64]. The BAMM analysis identifies lineages (at the genus level) exhibiting significant rate shifts in speciation, extinction and net diversification, and conducts a rate-through-time analysis of speciation, extinction and diversification shifts within the entire Berlinia clade. Incomplete sampling of the remaining species was accounted for by specifying genus-specific sampling fractions. Priors for BAMM were generated with BAMMtools v. 2.1 [65] in the R statistical environment [66]. The BAMM analysis was run with four Markov chains for 50 000 000 generations sampling every 5000 generations. Given the number of species included in our phylogenetic tree (152 species), we set the expected number of shifts to 1 following recommendations from the BAMM pipeline. The convergence of the likelihood and the number of shifts was deemed adequate when they reached 200 ESS or more. We removed 20% of the samples from the posterior as a burn-in distribution sampled by BAMM and analysed the output with BAMMtools. We computed 95% credible rate shift configurations, estimated the clade (focusing on the genus level) specific evolutionary rates by obtaining rates-through-time (RTT) plots (λ, μ and r) and obtained the visualization of the mean phylorate plots. In addition, we used the R package phytools v. 1.5-1 [67] to generate lineage-through-time plots to determine the temporal pattern of lineage accumulation in the Berlinia clade and its 16 genera. All tests were done on the dated phylogenetic tree obtained with BEAST.

(ii) Trait-dependent diversification rates: biomes and biome lability

To test the effect of the two biomes (forest and savanna) and the lability to shift these biomes at the genus level (labile and not labile) on diversification rates, we used the binary state speciation and extinction (BiSSE) model [68,69], where extinction and speciation rates are associated with the phenotypic evolution of a trait along a phylogeny. We used the dated tree obtained with BEAST and ran four independent MCMC chains for 10^5 steps for each of 10 randomly chosen trees using an exponential prior

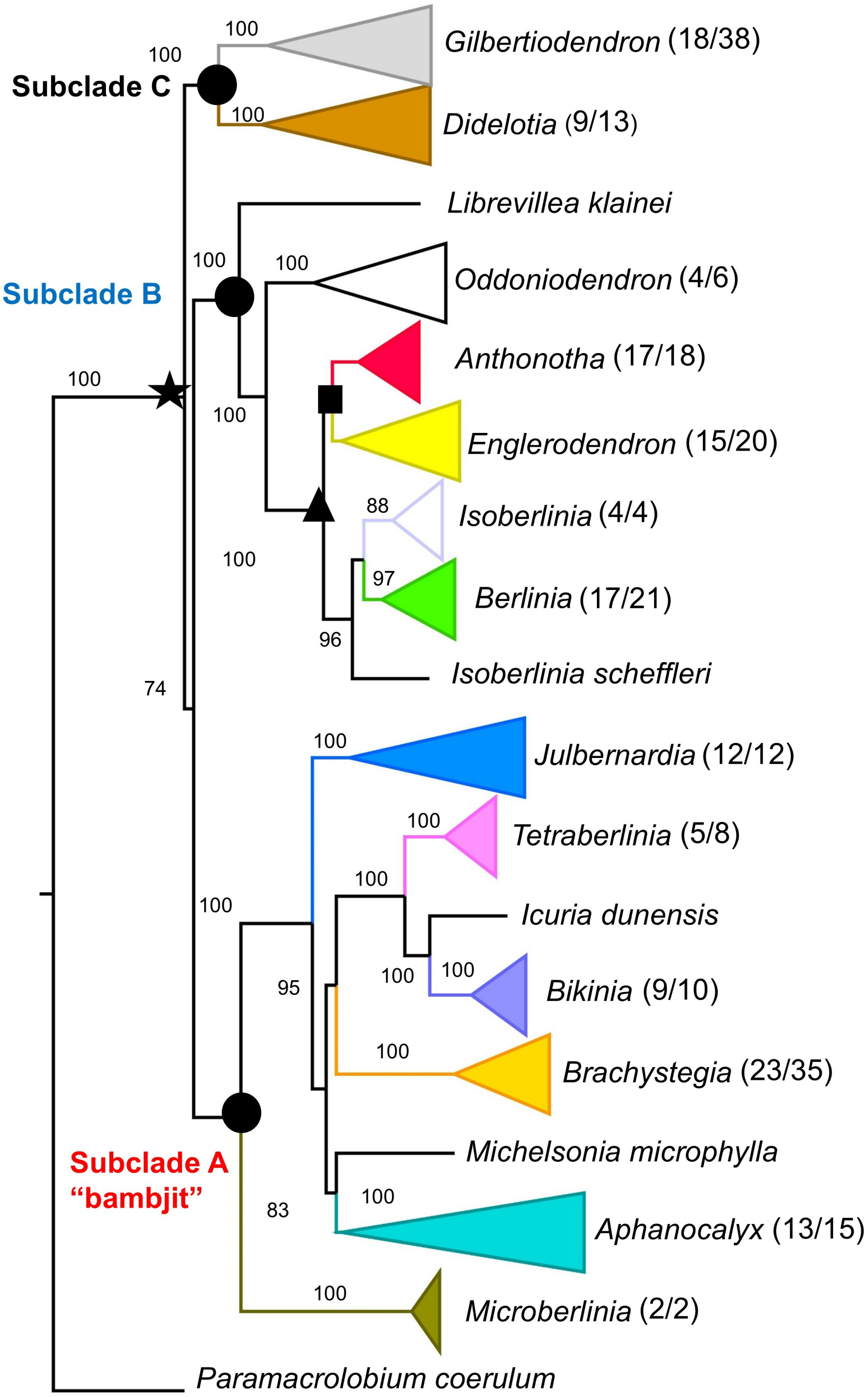

Figure 1. Phylogenetic relationships within the Berlinia clade based on maximum likelihood as implemented in RAxML and using the concatenated dataset. The major subclades recovered within the group are marked with black circles. The numbers in brackets represent the number of species sequenced/total on each genus. Values next to the branches represent bootstrap values. The triangle and the square indicate the placement of the fossils in the two approaches used in the calibration analyses. Square, restrictive approach: *Anthonotha* and *Englerodendron*, triangle, conservative approach: *Berlinia, Isoberlinia, Anthonotha* and *Englerodendron*

for the rates. We discarded the first 25% of steps of each chain as burn-in. We also tested differences in speciation rates between the two biomes and labile versus not labile genera using maximum likelihood (ML) and tested for significant differences among the models with ANOVA tests. Both ML and MCMC were run in the R package diversitree [69].

3. Results

(a) Phylogenomic reconstructions and major lineages within the Berlinia clade

The aligned matrix of 140 nuclear DNA sequences (orthologues) consisted of 56 605 bp, of which 22% were variable sites and 11% were parsimony informative sites (electronic supplementary material, table S2). The discarded genes (48%) were due to missing data or the identification of paralogy. We recovered similar topologies using ML, Bayesian and the multispecies coalescent tree with ASTRAL, obtaining highly resolved relationships among genera and within each of the 16 genera of the

Berlinia clade (figure 1; electronic supplementary material, figures S5). All genera within the Berlinia clade were recovered as monophyletic, except *Isoberlinia*, where *I. scheffleri* was found as sister to a clade comprising genus *Berlinia* sister to the remaining species of *Isoberlinia* included in this study (figure 1; electronic supplementary material, figures S5). The taxonomic status of *I. scheffleri* will be the subject of further investigation in a separate study.

(b) Biome shifts within the Berlinia clade

Nearly 80% of the species within the Berlinia clade were classified as inhabiting the forest biome (electronic supplementary material, table S3) and inferred the forest biome as ancestral. We found phylogenetic signal for the forest biome with the two metrics used: $\delta = 190.07$ (p-value = 0) and $D = -0.34$ (p-value = 0), suggesting that the forest biome is conserved in the Berlinia clade. However, our aggregation analysis suggests that the capacity to shift biomes (biome lability) is randomly distributed within the Berlinia clade at the genus level (p-value = 0.099). Biome lability was observed in six genera (*Berlinia*, *Julbernardia*, *Bikinia*, *Brachystegia*, *Isoberlinia* and *Aphanocalyx*), with nine independent transitions from forest to savanna (figure 2). We identified two distinct patterns of biome shifts. One pattern consisted in a single shift to savanna with subsequent diversification within the savanna lineages in *Brachystegia*, *Julbernardia* and *Isoberlinia* (excluding *I. scheffleri*). The second pattern consisted of single shifts to savanna within each genus, but without further diversification in the savanna lineages in *Bikinia*, *Aphanocalyx*, *Julbernardia* and *Berlinia*. In *Julbernardia* we found the two patterns occurring at different time scales (figure 3). We did not infer any biome shift in the remaining 11 genera, while these represent some of the most species-rich genera (e.g. *Berlinia*, *Gilbertiodendron*, *Anthonotha* and *Englerodendron*).

(c) Location and timing of biomes shifts among the major lineages within the Berlinia clade

Our dating analyses indicate that the Berlinia clade represents an ancient lineage that likely originated in the Eocene (*ca* 45 Ma), where all the crown ages of its extant genera originated from the Oligocene (figure 3; electronic supplementary material, table S4). As expected, we recovered older age estimates when we used the fossils to constrain only *Anthonotha* + *Englerodendron*. We thus report the most conservative age estimates that also are more congruent with age estimates of Detarioideae and the tribe Amherstieae. The shifts to the savanna biome occurred at two different time intervals, the earliest in the Oligocene in *Julbernardia* at about 26.56 Ma, and in the Miocene in *Isoberlinia* at 11.15 Ma (crown age 7.91 Ma) and *Brachystegia* at 9.7 Ma. These three early biome shifts were associated with subsequent diversification within the savanna biome. Thus, as the forest cover decreased, it seems that shifting to the newly available biome was only exploited early in the evolution of the Berlinia clade, and limited to subclades A and B. The other transitions we inferred to the savanna biome consisted of single shifts (without further diversification) and occurred from the late Miocene in *Julbernardia*, *Aphanocalyx* and *Berlinia*, during the Pliocene in *Bikinia*, and in the Pleistocene in *Berlinia* (figure 3).

(d) Diversification rates within the forest and savanna lineages

(i) Time-dependent diversification

Our analyses suggest an overall increase in species number within the Berlinia clade (figure 4A). Of the six models tested with RPANDA, we found a constant speciation rate with no extinction as the best supported model for our dataset (table 1). The lineages through-time plot indicates an increase of lineages since the late Eocene, with a marked increase from the late Miocene to the present (figure 4B). A more subtle increase in net diversification rates was inferred with BAMM from the late Eocene (figure 4C), due to an increased speciation rate with a constant extinction rate (electronic supplementary material, figures S6–S9). All our time dependent diversification analyses suggest an overall increase in net diversification within the Berlinia clade, both in forest and savanna lineages.

(ii) Biome and trait-dependent diversification rates

To test the effect of the two biomes (forest and savanna) and the lability to shift between these biomes at the genus level (labile and not labile) on diversification rates, we used the BiSSE approach using both a ML and a MCMC method. We did not find significant differences between a constant rate and an association with the biome ($\alpha = 0.05$, $p = 0.305$) or the lability to shift between biomes ($\alpha = 0.05$, $p = 0.172$), suggesting that these two attributes do not seem to be associated with changes in diversification rates. The posterior probabilities of the MCMC of speciation and extinction rates for both traits overlap and indicate no difference with a constant rate of speciation in the Berlinia clade (electronic supplementary material, figure S10).

4. Discussion

(a) Phylogenetic biome conservatism, but random distribution of biome lability

Phylogenetic biome conservatism is considered a major determinant of global biodiversity patterns [6]. Evidence at the community level [70,71] as well as large geographic scale analyses suggests a high prevalence of biome conservatism [3,4,7].

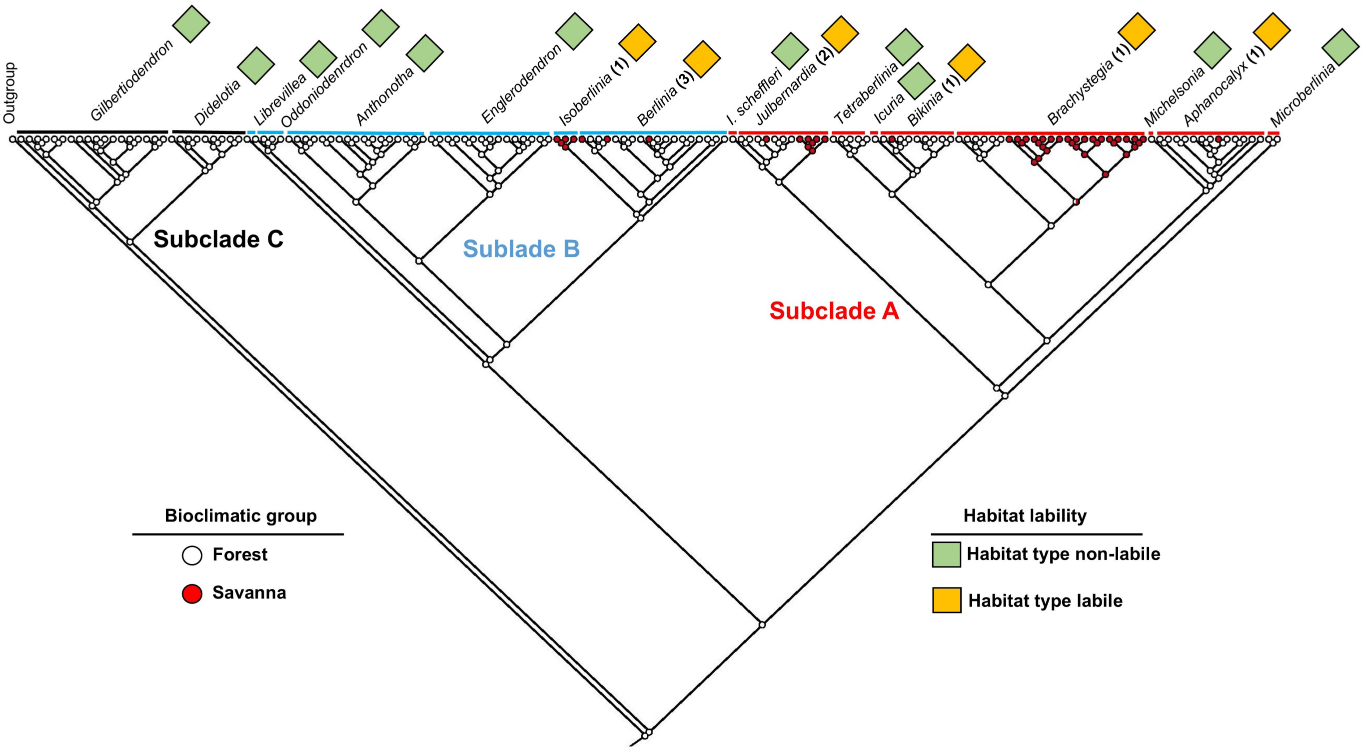

Figure 2. Distribution of the two biomes and biome lability within the Berlinia clade at the genus level. The colour in the circles at the tips and nodes indicate the (ancestral) biome. Green squares represent genera that remained in the forest biome, orange squares represent genera where shifts to the savanna biome occurred. The number in parenthesis indicates the number of transitions within each genus.

We found a similar trend within the Berlinia clade, as most of the genera within this group (11 of 16) have diversified within the same biome. In contrast to previous analyses based on genus-level phylogeny [17], our analysis provides a more detailed picture of the distribution of biome lability of African tropical trees at the species level. Our results support a previous finding of biome conservatism inferred at the genus level within the tribe Amherstieae using geographic distribution and climatic variables [72]. Our analyses indicate that the proportion of biome shift per speciation event in the Berlinia clade (6%) is very similar to the average estimated for tropical trees in Africa (7%) [17], or in the tribe Mimoseae (5%) [9], but lower than in the subfamily Cercidoideae (11–15%) [10] and higher than for plant lineages in the Southern Hemisphere (4%) [6]. We found no reversals to the forest biome once a lineage has shifted to savanna. Although our biome classification (forest, savanna) might have missed some finer subdivisions [17], our main conclusions should be robust because only a few species could be reclassified into additional biomes (e.g. montane within the forest biome or and seasonally dry forest within the savanna biome).

Our dating and ancestral reconstruction analyses suggest that the Berlinia clade probably originated in the forest biome during the Eocene (*ca* 45 Ma). Our results suggest that several genera within subclades A and B probably had formerly wider distribution ranges, retained their ancestral biome over long evolutionary time frames, and followed the contraction of the forest biome. For example, there are no extant members of *Anthonotha* and *Englerodendron* in Ethiopia or Kenya, where early Miocene fossils of these genera have been reported [46,47]. Thus, *Anthonotha* and *Englerodendron* do not seem to have exploited the availability of new drier habitat types in East Africa. Forests in East Africa were progressively disrupted starting from the early Miocene and often gradually replaced by deciduous forest and woodlands [52]. Almost all extant species of *Anthonotha* and *Englerodendron* are currently distributed in the Guineo-Congolian region in central Africa [38,39]. Our findings thus suggest that there are some genera within the Berlinia clade that seem to inherently lack the capacity to exploit drier new available habitats; however, our results demonstrate that this capability seems to be randomly distributed within the Berlinia clade. An alternative explanation is that shifts to other biomes occurred in these genera, but the resulting species went extinct later; however, no fossil record of woodland or savanna habitats supports this latter interpretation [73]. Wood fossils from the Miocene identified as *Brachystegia* from Ethiopia [74] and pollen fossils of *Isoberlinia*-type and *Brachystegia* from the Oligocene from the northern Ethiopian plateau [51,75] probably represent crown members of forest lineage of *Brachystegia* or stem members of the subclade B in the case of the *Isoberlinia*-type, rather than crown members of extant miombo woodlands [53].

(b) Timing of biome shifts and diversification patterns in the Berlinia clade

The dating estimates of our current study of the Berlinia clade contain the most complete representation of extant species to date and using two recent fossils (leaves) unequivocally assigned to two genera of the Berlinia clade. Our estimation of the origin of the Berlinia clades in the middle Eocene (45 Ma) is older (figure 3; electronic supplementary material, figure S11) than a previous estimate based on a limited representation and using a secondary calibration [22]. The Berlinia clade is one of the most derived lineages within the tribe Amherstieae [24] and our age estimates suggest that it diverged not long after the origin of the tribe

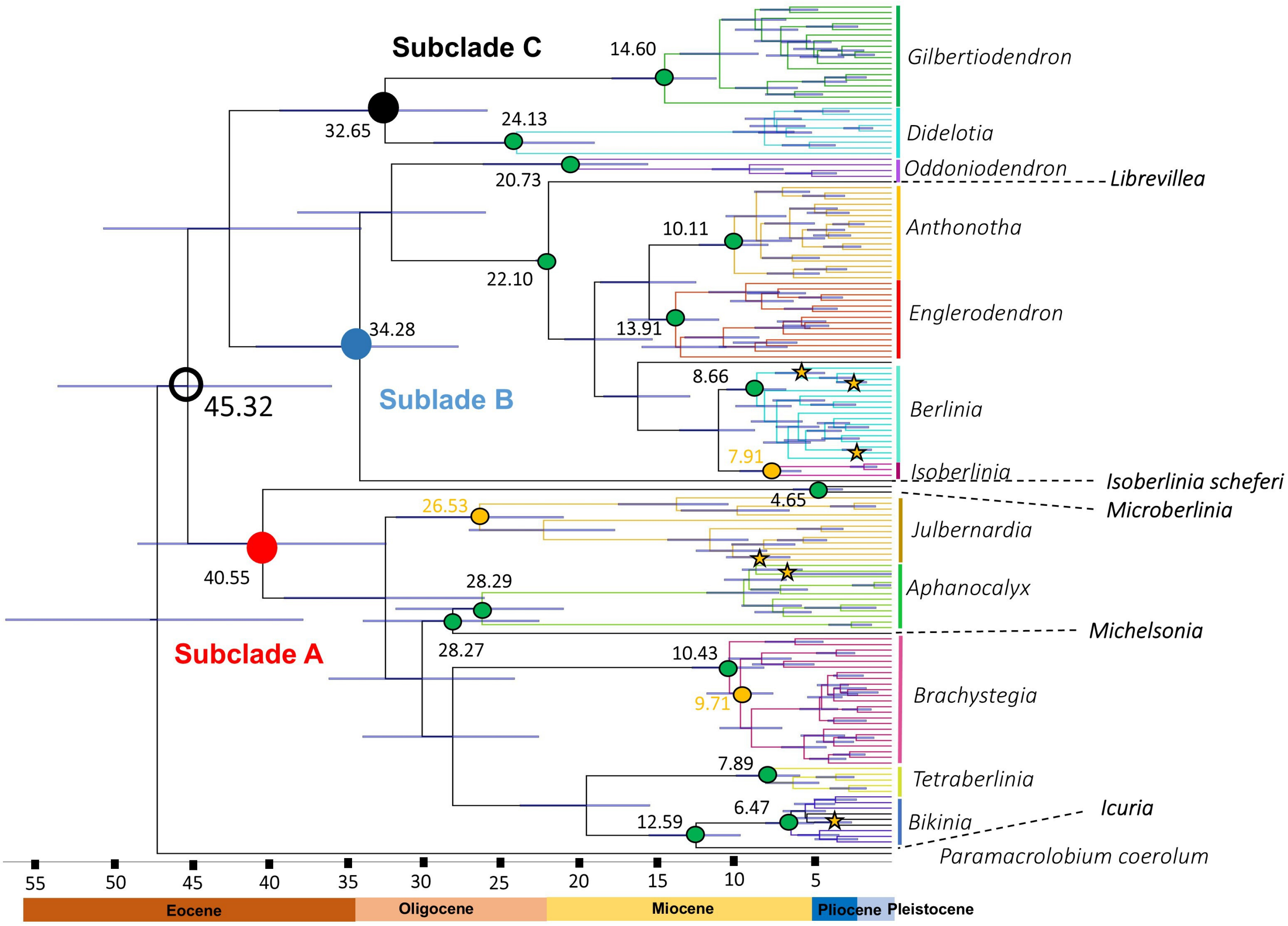

Figure 3. Time calibrated phylogenetic tree of the Berlinia clade obtained from the BEAST analysis. The blue bars indicate 95% posterior distribution of the age estimates. The green circles indicate the time of the origin (crown age) of the main forest lineages (genera) and the orange circles the time of the origin of savanna lineages that diversified within this biome. Orange stars indicate shifts from forest to savanna habitats without further diversification in the savanna biome. Genera in bold indicates the palaeoendemic lineages (mostly monotypic lineages).

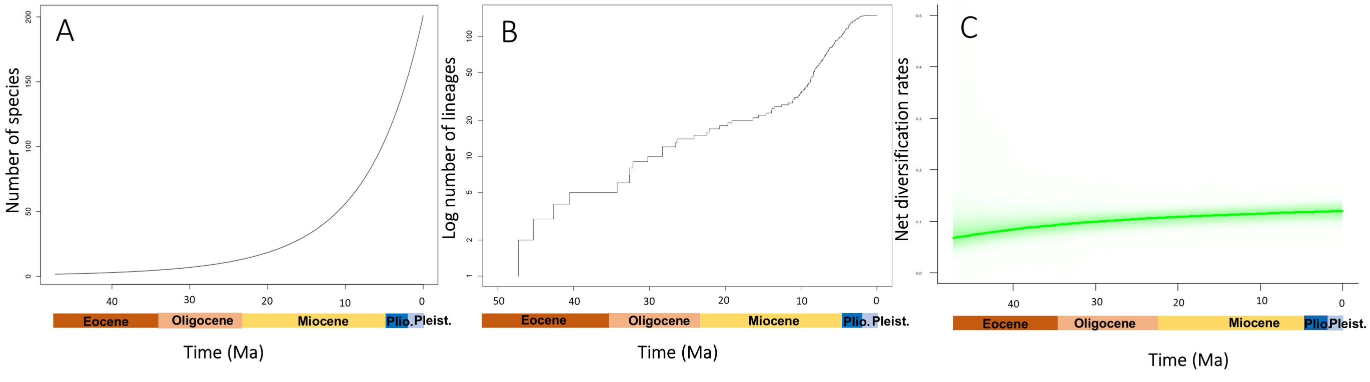

Figure 4. Diversification rates of the Berlinia clade based on (A) RPANDA, (B) LTT plots and (C) BAMM.

Amherstieae (estimated crown age 50 Ma) [45]. Our more conservative dating approach of the Berlinia clade is also in agreement with the fossils that have been assigned to genera within the tribe Amherstieae ranging in age between 20 and 46 Ma [48,51,53,55,73].

The early/middle Miocene has been suggested as a critical period in the transition from African rainforest biome to woodland/savanna landscapes [76]. Data from pollen and carbon isotopes from West and East Africa suggest that the grass-dominated savanna biome began to expand in the middle Miocene (16 Ma) and became widespread in the late Miocene (8 Ma) [77]. The conventional view has been that the open habitats of this period were dominated by C3 lineages, and that the dominance of C4 grasses did not occur until later, at around 10 Ma [78]. Indeed, plant leaf wax carbon isotopic composition ($\delta^{13}C_{wax}$) and pollen data suggest that the initial expansion of grassland habitats in the late Miocene of northeast Africa were dominated by C3 grasses, rather than C4 grasses [79]. Also, palaeobotanical data suggest that C3 wooded grassland, and woodland ecosystems dominated the North and East African landscapes before C4 grasses expanded. However, a recent study using several fossil sites in East Africa has challenged the previous conventional view and indicates that in the early Miocene (between 21 to 16 Ma) C4 grasses were abundant and contributing to the variety of heterogeneous habitats present during that period, including

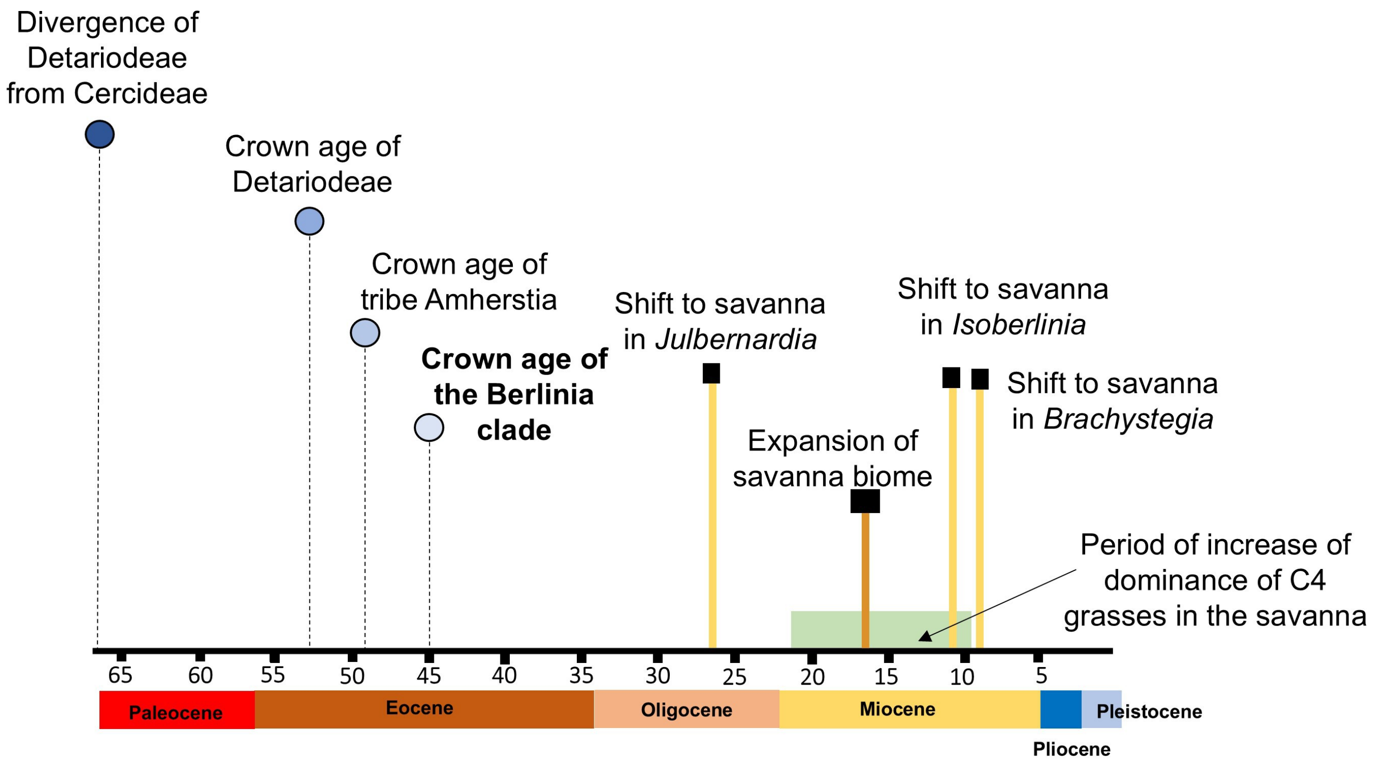

Figure 5. Diagrammatic representation of the estimated times of age of divergence and crown ages of the subfamily Detarioideae [44,45], tribe Amherstieae in relation to our estimation of the age of the Berlinia clade. The three single shifts to savanna in *Julbernardia*, *Isoberlinia* and *Brachystegia* are also contextualized with the expansion of the savanna biome and the dominance of C4 grasses [78,79].

Table 1. Results of the models tested with RPANDA in the Berlinia clade. Values in bold indicate the best-fitted model for the data. LH, log-likelihood; AICc, corrected Akaike information criterion; ΔAICc, change in AICc compared with the model with the lowest AICc; Models' parameters: λcon, speciation constant; λexp, speciation exponential; λlin, speciation linear; µ0, no extinction; µcon, constant extinction.

models	LH	AICc	ΔAICc
time-dependent			
λ_{con} and μ_0	**−326.45**	**654.45**	0.00
λ_{exp} and μ_0	−326.18	656.45	2.00
λ_{lin} and μ_0	−326.12	656.33	1.88
λ_{con} and μ_{con}	−326.54	655.11	0.66
λ_{exp} and μ_{con}	−326.18	658.53	4.08
λ_{lin} and μ_{con}	−326.25	656.58	2.13

wooded grasslands [80]. Our findings suggest that the shift to the savanna biome (stem age) in *Julbernardia* in the Oligocene (26.5 Ma) predated the emergence and dominance of C4 grasses in the early Miocene, while the shifts to *Isoberlinia* (11.15 Ma) and *Brachystegia* (9.7 Ma) occurred later, likely once the savanna biomes were dominated by C4 grasses (figure 5). Thus, our results provide a more complete framework of the emergence and diversification of the three extant dominant genera of extant miombo woodlands, suggesting that *Julbernardia* might have a more prominent role during the formation of savanna landscapes compared with species of *Brachystegia* and *Isoberlinia* that originated later [53]. Our results suggest an older age estimate for the origin and diversification of the dominant extant miombo *Brachystegia* previously inferred between 3 and 5 Ma with a limited representation of extant genera within the Berlinia clade [81,82].

We did not find evidence that biome shifts have prompted higher diversification rates in the Berlinia clade, similar to other findings of habitat shifts in Melastomataceae [83] and Malvaceae [84].

(c) Monotypic forest palaeoendemic genera with restricted distribution

We recovered three major lineages (subclades A–C), congruent with previous results on their taxonomic relationships [40] and with previous phylogenetic analyses based on a more limited representation of the group [22,23,39]. Our analyses revealed five monotypic genera (including *Isoberlinia scheffleri*), as well as *Microberlinia* with two extant species that originated between the Oligocene and Miocene (34–12 Ma) (figure 3). These phylogenetically isolated species are all restricted to the forest biome and most of them with limited distribution in tropical Africa (e.g. *Librevillea klanei* is restricted to western tropical Africa, *Isoberlinia scheffleri* is endemic to Tanzania and *Icuria dunensis* is restricted to Mozambique). Overall, our results suggest that the entire Berlinia clade has experienced low extinction rates, including the palaeoendemic lineages (mostly monotypic genera) we identified (electronic supplementary material, figures S7–S9). However, these forest palaeoendemic lineages seem to have slightly lower net diversification rates than lineages that shifted to new habitats (electronic supplementary material, figure S9). However, it is worth noticing that these mainly monotypic taxa might have experienced higher extinction rates than the species-rich genera in the Berlinia clade, which we were not able to differentiate with the methods we used in this study. *Paramacrolobium coeruleum*, sister to the Berlinia clade, is also a monotypic genus native to the forest biome but with a much wider distribution than *Librevillea*, *Icuria*, *Microberlinia*, *Michelsonia* and *Isoberlinia scheffleri*. The current distribution of *P. coeruleum* includes western, central and eastern Africa, from Guinea in the west to Kenya and Tanzania in the east, and south to Angola [85]. It is thus plausible that the ancestral lineage of the Berlinia clade and *P. coeruleum* also inhabited the forest biome. We found that the diversification rates were lower before the early Miocene in the entire Berlinia clade (figure 4B), and that forest lineages (e.g. *Berlinia* and *Anthonotha*) and savanna lineages (e.g. *Brachystegia*) that originated after this period seem to have increased net diversification rates. This supports a previous report showing that the lowland rain forest region in tropical Africa is characterized by old lineages that have persisted in these stable environments [20].

Despite the long evolutionary history of the Berlinia clade and the availability of new habitats during the multiple instances of forest contraction and expansion since the Miocene [18], some genera have only persisted in the forest biome. Thus, our study identified lineages that would be potentially more susceptible to reductions or modifications of the forest biome due to future climate change and land use alterations. For example, future land use and land cover projections under the RCP 8.5 ('worst case scenario') predicts a 5.6% area reduction of the Congolian rainforest in Central Africa due to cropland replacement, and an 8% due to climate change [12]. Trees in the Berlinia clade are long lived species with long generation times, and climate change will probably outpace the capacity for adaptation in lineages with biome lability. Additional fine-scale analyses at the population level within each species can provide a more detailed picture of the genetic diversity, demographic history and evolutionary potential for lineages with biome conservatism and palaeoendemic taxa.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All DNA sequences are deposited in the NCBI BioProject PRJNA472454 and the alignment of DNA sequences are deposited in Figshare [86]. Supplementary material is available online [87].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.O.: conceptualization, data curation, formal analysis, investigation, methodology; S.C.: conceptualization, data curation, investigation, methodology, writing—original draft, writing—review and editing; A.-P.G.: formal analysis, writing—review and editing; G.D.: formal analysis, writing—review and editing; A.D.P.: investigation, writing—review and editing; S.V.A.: data curation, resources, writing—review and editing; A.F.B.: data curation, resources, writing—review and editing; F.F.: investigation, resources, writing—review and editing; M.d.l.E.: resources, writing—review and editing; T.M.: writing—review and editing; O.J.H.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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