

SPECIAL ISSUE: AFRICAN FLORA IN A CHANGING WORLD

Sequential diversification with Miocene extinction and Pliocene speciation linked to mountain uplift explains the diversity of the African rain forest clade Monodoreae (Annonaceae)

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- **Background and Aims** Throughout the Cenozoic, Africa underwent several climatic and geological changes impacting the evolution of tropical rain forests (TRFs). African TRFs are thought to have extended from east to west in a 'pan-African' TRF, followed by several events of fragmentation during drier climate periods. During the Miocene, climate cooling and mountain uplift led to the aridification of tropical Africa and open habitats expanded at the expense of TRFs, which probably experienced local extinctions. However, in plants, these drivers were previously inferred using limited taxonomic and molecular data. Here, we tested the impact of climate and geological changes on diversification within the diverse clade Monodoreae (Annonaceae) composed of 90 tree species restricted to African TRFs.
- **Methods** We reconstructed a near-complete phylogenetic tree, based on 32 nuclear genes, and dated using relaxed clocks and fossil calibrations in a Bayesian framework. We inferred the biogeographical history and the diversification dynamics of the clade using multiple birth–death models.
- **Key Results** Monodoreae originated in East African TRFs ~25 million years ago (Ma) and expanded toward Central Africa during the Miocene. We inferred range contractions during the middle Miocene and document important connections between East and West African TRFs after 15–13 Ma. Our results indicated a sudden extinction event during the late Miocene, followed by an increase in speciation rates. Birth–death models suggested that African elevation change (orogeny) is positively linked to speciation in this clade.
- **Conclusion** East Africa is inferred as an important source of Monodoreae species, and possibly for African plant diversity in general. Our results support a 'sequential scenario of diversification' in which increased aridification triggered extinction of TRF species in Monodoreae. This was quickly followed by fragmentation of rain forests, subsequently enhancing lagged speciation resulting from vicariance and improved climate conditions. In contrast to previous ideas, the uplift of East Africa is shown to have played a positive role in Monodoreae diversification.

Key words: Annonaceae, aridification, biogeography, birth–death models, diversification, East Africa, forest fragmentation, macroevolution, tropical rain forests. Madagascar, Dahomey Gap

INTRODUCTION

Tropical rain forests (TRFs) are one of the more biodiverse ecosystems on Earth. Covering just 7 % of the land area, they contain over half of the world's biodiversity (Wilson, 1988; Eiserhardt *et al.*, 2017). After the Amazon basin, the Guineo-Congolian region of Africa contains the second largest continuous extent of TRF in the world (Malhi *et al.*, 2014). The African TRFs are divided in two major forested blocks: West-Central and East TRFs (Fig. 1; Olson *et al.*, 2001; Couvreur *et al.*, 2008; Droissart *et al.*, 2018; Brée *et al.*, 2020). The West-Central block is divided into two smaller blocks separated by the Dahomey gap located in Benin. The current distribution of TRFs across the continent is thought to be the result of various climatic and tectonic events that have shaped the distribution and evolution of African TRFs biodiversity (Morley, 2000; Couvreur *et al.*, 2021). A recent review identified six major

geo-climatic periods affecting the evolution of tropical Africa biodiversity (Couvreur *et al.*, 2021). In particular, the Miocene (~23–5.3 million years ago, Ma) is considered crucial in terms of diversification of the African flora (Plana, 2004; Couvreur *et al.*, 2021). For example, temperature increased during the middle Miocene Climatic Optimum (MMCO, ~17–14.7 Ma) and TRFs expanded across tropical Africa due to a warmer and moister climate (Morley, 2000, 2011). Then, from the middle Miocene Climatic Transition (MMCT, ~15–13 Ma), global temperatures and $p\text{CO}_2$ dropped (Zachos *et al.*, 2008; Westerhold *et al.*, 2020). These climate changes, as well as the uplift of East Africa, led to the aridification of Africa throughout the Miocene (Sepulchre *et al.*, 2006; Herbert *et al.*, 2016) favouring the expansion of open, grass-dominated habitats (Retallack *et al.*, 1990; Morley, 2000; Jacobs, 2004; Senut *et al.*, 2009). From 10 Ma, palaeo-vegetation records show an increasing percentage of C_4 plants until the present (Ségalen *et al.*, 2007; Uno *et al.*,

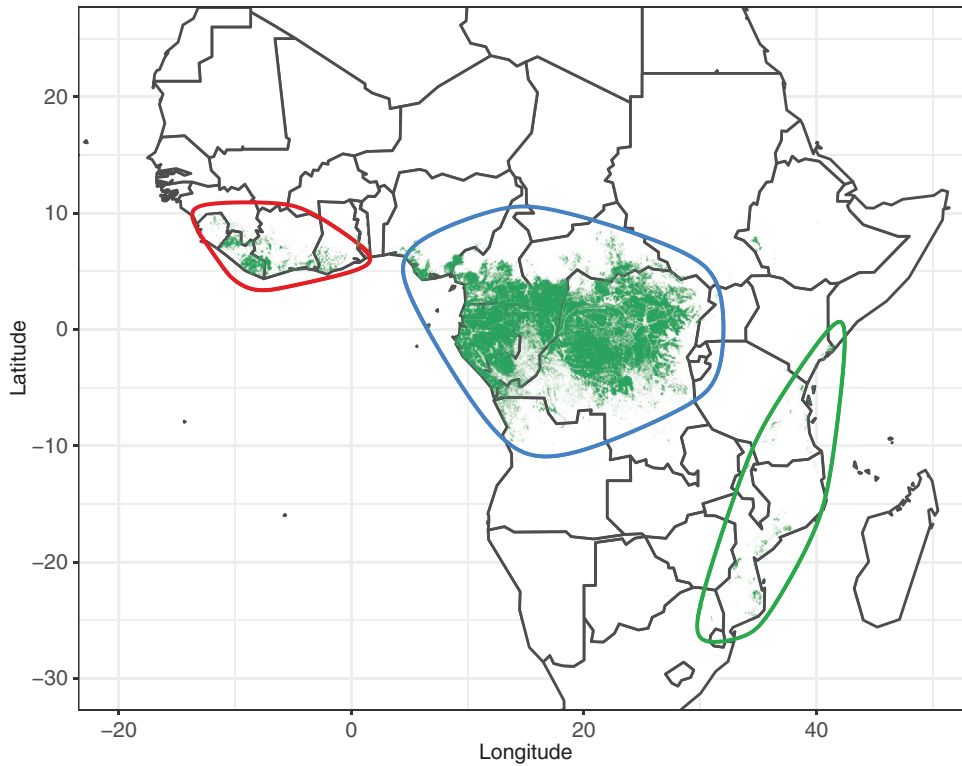


FIG. 1. Map of the tropical rain forest of Africa (after [Mayaux et al., 2004](#)): Western block (red), Central block (blue), Eastern block (green) and Madagascar (yellow).

2016; [Polissar et al., 2019](#)) and increases in diversification rates of herbaceous plants such as Poaceae and Asteraceae ([Kergoat et al., 2018](#); [Palazzesi et al., 2022](#)), indicating increasing dominance of grasslands across Africa. While open grassland expanded, TRFs contracted across its distribution ([Plana, 2004](#)). This contraction is suggested to have led to vicariance events within TRF clades before the MMCT, as detected in several phylogenetic studies ([Couvreur et al., 2008](#); [Dimitrov et al., 2012](#); [Menegon et al., 2014](#); [Brée et al., 2020](#)). As drier habitats expanded, some forest-adapted clades experienced habitat shifts towards drier habitats during the Miocene ([Davis et al., 2002](#); [Bouchenak-Khelladi et al., 2010](#); [Armstrong et al., 2014](#); [Tosso et al., 2018](#); [Veranso-Libalah et al., 2018](#)). In the early Pliocene (~5.3–3.6 Ma), the climate became warmer and moister ([Haywood et al., 2013](#)) and the TRFs re-expanded while savannas contracted ([Morley, 2000](#); [Plana, 2004](#)), suggesting reconnection of the West-Central and East TRF blocks ([Fer et al., 2017](#); [Joordens et al., 2019](#)).

These climatic changes and rain forest dynamics gave rise to one of the major hypotheses explaining the distribution of TRF clades in Africa: the fragmentation–refugia mechanism ([Couvreur et al., 2008, 2021](#); [Pokorny et al., 2015](#)). This mechanism links multi-million-year climatic fluctuations and continent-wide expansion–contraction of TRF dynamics to numerous vicariant speciation events in TRF-restricted clades ([Moritz et al., 2000](#); [Plana, 2004](#); [Loader et al., 2007](#); [Couvreur et al., 2008, 2021](#)). This suggests the existence of a ‘pan-African forest’ extending continuously from Western to Eastern Africa during favourable climatic times, and fragmenting into isolated Western-Central and Eastern blocks during drier climate periods ([Morley, 2000, 2011](#); [Plana, 2004](#);

[Couvreur et al., 2021](#)). The fragmentation–refugia mechanism was suggested to explain the present-day distribution patterns of some African TRF clades with species restricted to East or West-Central Africa in plants ([Davis et al., 2002](#); [Couvreur et al., 2008](#); [Brée et al., 2020](#)), butterflies ([Aduse-Poku et al., 2021](#)), birds ([Fjeldså et al., 2007](#); [Fjeldså and Bowie, 2008](#); [Voelker et al., 2010](#); [Huntley and Voelker, 2016](#); [Fuchs et al., 2017](#)), chameleons ([Tolley et al., 2013](#); [Nkommeneck et al., 2022](#)), frogs ([Bell et al., 2017](#); [Leaché et al., 2019](#)) and mammals ([Demos et al., 2014](#); [Bryja et al., 2017](#); [Nicolas et al., 2020](#)). To date, this biogeographical mechanism has been inferred based on few data ([Couvreur et al., 2008](#)) at the taxonomic and molecular marker sampling level, especially in plants. In particular, the number of vicariant events used to infer this mechanism was generally low ([Davis et al., 2002](#); [Couvreur et al., 2008](#); [Brée et al., 2020](#)).

Another major hypothesis explaining African TRFs diversity is the impact of extinction ([Morley and Richards, 1993](#); [Couvreur, 2015](#)). Under the environmental changes, contraction of the did not only triggered speciation via allopatric speciation, but also probably triggered extinction across TRF clades ([Morley and Richards, 1993](#); [Plana, 2004](#); [Aduse-Poku et al., 2021](#)). Major extinction events in TRF clades were suggested to have occurred at the Eocene–Oligocene boundary ~33.9 Ma ([Pan et al., 2006](#); [Faye et al., 2016](#); [Currano et al., 2021](#)), in the first half of the Miocene between 23 and 13.8 Ma ([Morley, 2000](#); [Couvreur, 2015](#)), in the late Miocene around 11.6 and 7.2 Ma ([Morley, 2011](#)), and in the late Pliocene ~3.6–2.58 Ma ([Morley, 2000](#); [Couvreur, 2015](#)). However, signal of past extinction in African TRF plants has rarely been tested with a comprehensive dated phylogeny (e.g. [Brée et al., 2020](#)).

The opposite view to these hypotheses is that speciation and extinction remained relatively constant through time. Indeed, African TRFs have lower extant species richness compared to TRFs from the Americas and from South-East Asia (Parmentier *et al.*, 2007; Couvreur, 2015). One of the hypotheses invoked to explain such a pattern is that diversification was rather constant in African TRFs, whereas American and South-East Asian TRFs experienced bursts of speciation (Gentry, 1982; Couvreur, 2015). This hypothesis has been supported by global-scale molecular studies of TRF clades showing no diversification shifts in the African lineages (Erkens *et al.*, 2012; Kissling *et al.*, 2012; Baker and Couvreur, 2013).

The bursts of speciation in the American TRFs are in part attributed to Andean uplift (Hoorn *et al.*, 2010; Lagomarsino *et al.*, 2016; Boschman and Condamine, 2022). Indeed, mountain uplift is generally linked to increased diversification, through various mechanisms such as the creation of new habitats or population isolation (Dimitrov *et al.*, 2012; Antonelli *et al.*, 2018; Muellner-Riehl, 2019; Rahbek *et al.*, 2019; Couvreur *et al.*, 2021). These topographical uplifts also have indirect effects via the modification of climate (Sepulchre *et al.*, 2006). In Africa, mountains harbour high levels of species diversity and endemism (Fjelds  and Lovett, 1997; Burgess *et al.*, 2007). East Africa, which has the highest topographical complexity compared to the rest of Africa, has been inferred to be rich in both neo- and palaeo-endemics (Dagallier *et al.*, 2020). Several geological uplifts occurred during the Cenozoic (Guillocheau *et al.*, 2018; Couvreur *et al.*, 2021), and the uplift of East Africa was documented to have started during the late Miocene (Griffiths, 1993; Sepulchre *et al.*, 2006; Macgregor, 2015; Couvreur *et al.*, 2021). However, the impact of mountain uplift on TRF clade diversification has never been tested.

The *Monodoreae* tribe is an African TRF-restricted clade of the plant family Annonaceae. The tribe contains, to date, 11 genera and 90 species (Dagallier *et al.*, in press) restricted to Africa, with one genus also occurring in Madagascar (*Isolona*). Species in *Monodoreae* show high levels of endemism across the discrete TRF blocks, occurring either in West-Central or East Africa, with a single species occurring across both blocks (Dagallier, 2021; Dagallier *et al.*, in press). To date, there is little knowledge about the mode of dispersal across the tribe. However, fruit morphology provides some indication about dispersal. Species of this tribe have large fruits (generally >3 cm long), most of them cauliflorous (i.e. growing on the trunk), lack the typical stipe at the base of each individual monocarp composing fruits in Annonaceae (van Setten and Koek-Noorman, 1992) and are generally dull-coloured, varying from brown, to green and orange. This fruit morphology suggests dispersal syndromes targeting mainly ruminant mammals (Gautier-Hion *et al.*, 1985). Indeed, some studies have shown that species of *Monodoreae* are included in the diet of TRF understory mammals such as gorillas, chimpanzees and forest elephants (Gautier-Hion *et al.*, 1985; Tutin and Fernandez, 1993; White *et al.*, 1993; Remis *et al.*, 2001; Rogers *et al.*, 2004). Cauliflorous fruits in particular limit plant dispersal because they target understory dispersers, which are relatively sedentary and habitat-specific (Onstein *et al.*, 2018, 2019). *Monodoreae* are thus unlikely to disperse over long distances (i.e. hundreds or thousands of kilometres), and especially not across different

habitats. Finally, very few species have adapted to dry conditions (e.g. *Hexalobus monopetalus*, Botermans *et al.*, 2011). Together, these data suggest that tribe *Monodoreae* is probably TRF-restricted with limited opportunities for long-distance dispersal, and thus is a good model to test hypotheses about TRF dynamics through time, in particular the fragmentation–refugia mechanism (Couvreur *et al.*, 2008).

Here we infer a near complete species-level dated phylogenomic tree of *Monodoreae* to test: (1) if the ancestral range of the tribe extended across Africa, supporting the existence of a pan-African rain forest as suggested under the fragmentation–refugia mechanism; (2) if multiple discrete and synchronous speciation events occurred between major forest blocks and if they coincided with increased climatic aridity in Africa leading to TRF fragmentation; (3) if diversification was constant, or if TRFs experienced major increases or decreases of diversification, or sudden extinctions; and (4) if diversification was associated with changes in palaeotemperature, proportion of C₄ plants or elevation linked to mountain uplift.

MATERIAL AND METHODS

Taxon sampling and species distribution

Species delimitation within *Monodoreae* was previously investigated and validated using a densely sampled phylogenetic tree and morphology (Dagallier, 2021; Dagallier *et al.*, in press). This led to the description of several new species and the placement of two genera within the new tribe Ophrypetaleae. Here, we sampled 88 of the 90 known species of *Monodoreae* (97.8 % of the total species richness). Differences in species number with Dagallier (2021) where 92 species of *Monodoreae* were reported are due to recent changes: the name *Uvariopsis sessiliflora* is now a synonym of *U. dioica*, and ‘*U. sp. nov. 1 Uganda*’ has yet to be formally described due to limited morphological data (Dagallier *et al.*, in press). One specimen per species was sampled, except in the following two cases. In cases of species with described varieties or subspecies, one specimen per variety or subspecies was sampled. Most of the species are geographically restricted to one of the following regions: East Africa, West Africa, Central Africa, or West and Central Africa. In the case of species distributed in more than one region, we included one specimen per region when possible. Our dataset also comprised outgroups within the Annonaceae from different closely related tribes, such as the Ophrypetaleae (see Dagallier, 2021; Dagallier *et al.*, in press) and Uvarieae tribes, and from more distantly related tribes (Malmeoideae, Annonoideae). We also included one specimen of the genus *Anaxagorea* which is the earliest diverging Annonaceae genus (Couvreur *et al.*, 2019), and one specimen of Eupomatiaceae (*Eupomatia*), which is the sister family of Annonaceae (Sauquet *et al.*, 2003). Details on the vouchers used in this study can be found in Supplementary Data Table S1. DNA extractions and library preparations were done following the protocols described in Couvreur *et al.* (2019), Dagallier (2021) and Dagallier *et al.* (in press). DNA was sequenced on an Illumina HiSeq 2500 with paired-end reads of 150 bp.

Molecular dataset

For each specimen in our dataset, we retrieved cleaned reads from previous analyses (Dagallier, 2021; Dagallier *et al.*, in press). These reads were then processed and assembled using HybPiper 1.3.1 (Johnson *et al.*, 2016). The reads were aligned to the reference (i.e. the sequences of the 469 nuclear genes targeted) using Burrow–Wheeler Alignment (Li and Durbin, 2009) and sorted according to the targeted gene. Reads were then assembled into contigs using SPAdes (Bankevich *et al.*, 2012). Contigs were then aligned to the reference and intron sequences were then generated partially (or completely in case of short introns). Finally, the contigs and the introns were assembled into supercontigs (later also called ‘genes’ or ‘loci’), i.e. reconstructed genes with multiple exons and partial introns.

The sequences of each gene were then aligned using MAFFT 7.305 (Katoh and Standley, 2013) using the automatic selection of the alignment algorithm (parameter ‘--auto’). Poorly aligned regions were cleaned using Gblocks 0.91b (Talavera and Castresana, 2007), and the alignments were filled with gaps so that all the sequences in the alignment have the same length and so that every species is included in the alignment. We filtered the dataset to retain only genes for which the exon sequences mapped at least at 75 % of the reference gene and that were retrieved in 75 % of the species (75/75 dataset).

HybPiper also includes a tool that flags some of the retrieved genes as potential paralogues where different contigs targeted the same reference gene with similar coverage depth (i.e. meaning that variants of the same gene may occur). We executed an exploratory maximum-likelihood phylogenetic reconstruction of these putative paralogues using RAxML 8.2.9 (Stamatakis, 2014), and examined the reconstructed phylogeny to check whether the variants of the genes formed two clear clusters of species. If so, the alignment for this gene was discarded from the dataset.

Using Bayesian inference (BI) to simultaneously infer phylogenetic relationships and divergence times allows us to explicitly incorporate topological and age uncertainties. However, the use of BI with hundreds of genes is computationally impossible to achieve in a reasonable time. We thus applied a ‘gene shopping’ approach to select a subset of the most clock-like genes to ease convergence and reduce the computational time (Smith *et al.*, 2018). We first reconstructed a maximum-likelihood phylogenetic tree with RAxML for each gene. Each gene tree was then rooted with the outgroup *Eupomatia* using phyx (Brown *et al.*, 2017) and we calculated the root-to-tip variance of the trees using SortaDate (Smith *et al.*, 2018). We then selected a subset composed of the 32 most clock-like genes, that is the 32 genes with the lowest root-to-tip variance. This gene selection strategy has already been used to infer dated phylogenetic trees in Annonaceae (Brée *et al.*, 2020; Helmstetter *et al.*, 2020). Note that we tried with a higher number of genes, but BEAST could not run. For each of these 32 genes, we inferred the best fitting substitution model using ModelTest-NG based on the Bayesian Information Criterion (Darriba *et al.*, 2020).

Phylogenetic reconstruction and molecular dating

We simultaneously reconstructed and dated the phylogenetic tree of *Monodoreae* using BEAST 2.6.4 (Bouckaert *et al.*,

2019). The alignment of the 32 selected genes (see above) was first converted from fasta to nexus format using PGDSpider (Lischer and Excoffier, 2012) and was assigned a molecular partition in BEAUTi (Bouckaert *et al.*, 2019). Substitution models were defined for each gene following the best model retrieved by ModelTest-NG (see Supplementary Data Table S2) with no estimation of the substitution rate.

To calibrate the molecular clock, we relied on primary fossil calibrations to provide age priors at specific nodes. First, the fossil *Endressinia brasiliensis* is a leafy shoot dated from the Aptian–Albian boundary (113.4–112.6 Ma), which confers a maximum age for the crown node of Magnoliineae (i.e. including Annonaceae and Eupomatiaceae) as shown by its phylogenetic placement (Massoni *et al.*, 2015b). Second, the fossil *Futabanthus asamigawaensis* is a flower dated from the early Coniacian (~ 89 Ma) and provides a minimum age for the crown node of Annonaceae (Pirie and Doyle, 2012). We thus constrained the root of the tree (i.e. Annonaceae + Eupomatiaceae) with a hard upper bound at 112.6 Ma and we set a wide uniform prior from 89 to 112.6 Ma on the crown Annonaceae (see nodes marked with an orange triangle in Supplementary Data Fig. S1).

We set the tree prior as the Yule (pure birth) model, and the clock model as the uncorrelated log-normal (UCLD) model (Drummond *et al.*, 2006) with estimation of the clock rate. We ran four Markov chain Monte Carlo (MCMC) in parallel, running for 500 million generations each, sampling every 50 000 generations. We evaluated the convergence of the MCMC with the effective sampling size (ESS) using Tracer 1.7 (Rambaut *et al.*, 2018). We then used TreeAnnotator to draw the maximum clade credibility (MCC) tree, and to compute the mean node ages, the 95 % highest posterior density (HPD) of node ages and the posterior probability (PP) for each node, after discarding the burn-in. We then pruned the dated MCC tree to keep only the *Monodoreae* tribe and perform downstream analyses.

Biogeographical history

To reconstruct the ancestral ranges of the *Monodoreae* and to identify vicariant events, we relied on the Dispersion–Extinction–Cladogenesis (DEC) model (Ree and Smith, 2008) as implemented in the *BioGeoBEARS* R package (Matzke, 2014). We did not run the DEC + J model because founder events (or colonization of new ranges via jump dispersal without intermediate widespread dispersion) are very unlikely in *Monodoreae* due to their low dispersal abilities (see Introduction), and because the DEC + J model inflates the contribution of time-independent cladogenetic events to the likelihood of the model (Ree and Sanmartín, 2018).

First, we assigned each *Monodoreae* species to a geographical area, corresponding to a TRF region (Fig. 1) in which the species are currently distributed (West Africa, Central Africa, East Africa or Madagascar). Most of the species were assigned to a single region (endemic range), but some of them were assigned to a widespread range (e.g. West-Central Africa). We restricted the allowed ranges to West (W), Centre (C), East (E), Madagascar (M), West-Centre (WC), Centre-East (CE), East-Madagascar (EM) and West-Centre-East (WCE) and constrained the maximum number of areas per ancestral range to three. We

also defined an ‘area adjacency’ matrix in which Madagascar is only adjacent to East-Africa, and defined the dispersal probabilities between areas to one, except for the dispersal probabilities from and to Madagascar that were set to zero, and the dispersal from East to Madagascar that was set to 0.1.

The marginal probabilities of each range were then plotted on the ancestral nodes and we considered the most likely ancestral range as the one having the highest marginal probability. We then considered several biogeographical events to occur at the ancestral nodes. A branch starting at an ancestral node with an endemic range (W, C, E or M) leading to at least one daughter node with a widespread range (WC, CE, EM or WCE) was considered as a range expansion (like ‘dispersal’ in BioGeoBEARS). A branch starting at an ancestral node with widespread range (WC, CE, EM or WCE) leading to one daughter node with an endemic range (W, C, E or M) was considered as a range contraction (‘sympatry subset’ in BioGeoBEARS). Finally, an ancestral node with widespread range (WC, CE, EM or WCE) leading to two daughter nodes with a different endemic range each (W, C, E or M) was considered as a vicariance event (‘vicariance narrow’ in BioGeoBEARS). The branches (for range expansion or range contraction events) and nodes (for vicariance events) at which each of these events occurred were then plotted.

Diversification analyses

Testing for branch- and clade-specific diversification rates. To test for diversification rate shifts across the reconstructed tree, we used three different methods designed to estimate the branch- or clade-specific speciation and extinction rates. The net diversification rate is defined as speciation minus extinction (later referred to as ‘diversification rate’). The use of several different models allows us to cross-check the estimations (Condamine et al., 2018). Nonetheless, it is worth mentioning that each method differs at several points in the way speciation and extinction rates are estimated.

First, we used the cladogenetic diversification rate shift (CladS) model to estimate branch-specific diversification rates. CladS implements a birth–death model where speciation rates are inherited at a speciation event, but with a shift drawn from a probability distribution parameterized with the parental rates (Maliot et al., 2019). The extinction rate also varies across branches, but the turnover (i.e. speciation divided by extinction) is constant across the branches. The model is then computed using data augmentation in an MCMC with three chains. To assess convergence, the Gelman statistics are then computed every 200 iterations and the chains stop when these statistics drop below 1.05. We used the CladS model as implemented in the PANDA Julia package (Maliot and Morlon, 2021).

Second, we used RevBayes to model the estimation of branch-specific diversification (speciation and extinction) rates (BSDR; Höhna et al., 2019). The BSDR model is a birth–death model that breaks time into small intervals and for which speciation and extinction rates can change at each time interval. The new speciation and extinction rates at a new interval are drawn from a lognormal distribution. To ease the computation, the lognormal distribution is approximated using discrete rate categories. We set up the model following the RevBayes tutorial (available at: [https://revbayes.](https://revbayes.github.io/tutorials/divrate/branch_specific.html)

[github.io/tutorials/divrate/branch_specific.html](https://revbayes.github.io/tutorials/divrate/branch_specific.html)). The parameters were then estimated using two reverse-jumping MCMC (rjMCMC) of 4000 iterations each, sampling every 200 iterations. We performed several analyses with different sets of priors to check the consistency of the results between the different prior specifications. We set the discrete rate categories prior to 6 or 10, and the initial value of the number of expected rate shift to 1, 4 or 10. The convergence of the rjMCMC was checked with ESS > 200 using Tracer 1.7 (Rambaut et al., 2018).

Third, we used the Bayesian analysis of macroevolutionary mixtures (BAMM) to estimate the variation of speciation and extinction rates through time, but also to detect significant clade-specific shifts in these rates (Rabosky, 2014). BAMM uses rjMCMC to explore the space of parameters and the number of rate shifts. We set prior values using the *BAMMtools* R package (Rabosky et al., 2014), with an expected number of rate shifts equal to 1. We ran four rjMCMC for 10 000 000 generations, sampling every 10 000 generations. We then calculated the ESS of the log-likelihood and the number of shifts using the *coda* R package (Plummer et al., 2020) after discarding 10 % of burn-in to assess the convergence of the chains (ESS > 200).

Each of these three models accounts for the sampling fraction in the calculation of the parameters. For CladS and BAMM, we set the sampling fraction to be clade-specific, with every genus fully sampled (i.e. a sampling fraction of 1) except for *Uvariopsis* and *Lukea* having a sampling fraction of 0.85 and 0.5, respectively. For the BSDR model, we set the sampling fraction for the whole phylogeny at ~0.978.

Testing for sudden extinction events. To test whether the evolutionary history of the *Monodoreae* was impacted by one or several sudden extinction events, we used the compound Poisson process on Mass-Extinction Times model (CoMET; May et al., 2016) as implemented in the *TESS* R package (Höhna et al., 2016). This model estimates the tree-wide speciation and extinction rates, and the probability of several tree-wide events occurring, such as shifts in speciation rate, shifts in extinction rates or sudden extinction events (i.e. when several lineages go extinct with a prior probability). The speciation and extinction rates are constant between two events. The events are estimated under the independent compound Poisson process. Parameters are estimated using an rjMCMC over various episodic birth–death models. Model confidence is assessed by computing the Bayes factor (BF) between each model (May et al., 2016). For our CoMET analysis, we set the priors on the number of extinction events and number of expected changes to 2. Note that the prior on the number of events does not impact the results as the models are compared using BFs (Höhna et al., 2015). We performed ten different CoMET analyses with prior values on the survival probability to an extinction event ranging every 5 % from 5 to 50 %. The rjMCMC was run until the ESS for each parameter reached at least 500. We considered the support for a rate shift or for a sudden extinction event as substantially significant for $2\ln\text{BF} > 2$, as strongly significant for $2\ln\text{BF} > 6$ and as decisive for $2\ln\text{BF} > 10$ (Kass and Raftery, 1995; Höhna et al., 2015).

Testing the impact of the palaeoenvironment. To test if the diversification of the *Monodoreae* was associated with changes in past environmental variables (temperature, elevation variation

of the African continent, and proportion of C_4 plants in the African palaeoflora), we fitted several birth–death models that estimate the speciation and extinction rates along a continuous period of time in a maximum-likelihood framework. We set the models allowing the speciation and extinction rates to vary exponentially with time (time-dependent models) or exponentially with environmental variables (environment-dependent models) (Condamine *et al.*, 2013). We also fitted models with constant or null speciation and extinction rates. The best fitting model was then evaluated using the corrected Akaike Information Criterion (AICc). The complete list of models fitted is given in Table 1.

The environment-dependent models use environmental data spanning the time interval covered by the phylogenetic tree. Missing values were interpolated using the spline interpolation implemented in the *sm.spline* function from the *pspline* R package (Ripley, 2017). Past temperature at global scales was inferred from the widely used oxygen isotope data recovered from benthic foraminifer shells (Zachos *et al.*, 2008; Westerhold *et al.*, 2020). Past elevation change across the African continent was newly computed using the data from Scotese & Wright (2018). First, the geo-referenced occurrences of the *Monodoreae* species were extracted from the RAINBIO database (Dauby *et al.*, 2016), and the convex hull containing all the point coordinates was computed using the *chull* function from the *grDevices* R package. After conversion to *SpatialPolygonsDataFrame* object with the *sp* R package (Pebesma *et al.*, 2021), the intersection of the envelope with the African coastline was computed using the *gIntersection* function in the *rgeos* R package (Bivand *et al.*, 2020). Within this intersected envelope, we computed the geo-coordinates of every unique point with latitude and longitude

values at one degree precision (e.g. points with coordinates 10°N 10°E, 10°N 11°E, 10°N 12°E, etc.), and extracted the elevation value for each of these points every 5 million years (Myr) from the present to 30 Ma, using the reconstruct function in the *chronosphere* R package (Kocsis and Raja, 2021). We then computed the mean elevation for each time.

Finally, the proportion of C_4 plants in the African palaeoflora was taken from the reconstructions made by Pollisar *et al.* (2019) based on the composition of the ^{13}C isotope in plant waxes. To represent the proportion of C_4 plants in tropical Africa, we selected the data from the sites 959 (Guinean Gulf), 241 and 235 (East Africa). Given the oldest C_4 value at 23.38 Ma is very low compared to the values from 15 to 20 Ma (1.66 vs. 10.69–13.05), we replaced it by the lowest value found between 15 and 20 Ma (i.e. 10.69) to avoid distortion of the interpolation toward negative values. Moreover, as 23.38 Ma is younger than the clade age (25 Ma), we artificially duplicated the 10.69 C_4 value at 25.1 Ma (Supplementary Data Fig. S17).

The scripts for the biogeographical and diversification analyses carried out in this study are available at https://github.com/LPDagallier/Monodoreae_macroevolution.

RESULTS

Gene recovery

We recovered all 369 exons, at least partially, targeted by the Annonaceae bait kit (Couvreur *et al.*, 2019). After filtering and removal of paralogous loci, the 75/75 dataset contained 318 supercontigs. The 32 supercontigs most clock-like used for the

TABLE 1. Results of the environment-dependent birth–death models applied to the *Monodoreae* with RPANDA. When the rates are not constant, they vary exponentially with time or with the environmental variables (temperature = Temp, or elevation = Elev, or percentage of C_4 plants = PercC4). logL, log-likelihood; λ_0 , speciation rate; α , rate of variation in speciation according to the palaeo-environmental variable; μ_0 , extinction rate; β , rate of variation in extinction according to the palaeo-environmental variable.

Model	Speciation varies with:	Extinction varies with:	logL	AICc	λ_0	α	μ_0	β	ΔAICc
BDPercC4	C_4 proportion	C_4 proportion	−224.08	456.63	1.6829	−0.0439	2.1736	−0.0656	−12.66
BElev	Elevation	No extinction	−232.57	469.29	0.0017	0.0066	–	–	0
BElevDConst	Elevation	Constant	−232.63	471.55	0.0029	0.0059	0.0005	–	2.26
BTemp	Temperature	No extinction	−234.17	472.48	0.1255	0.0829	–	–	3.19
BConst	Constant	No extinction	−235.75	473.55	0.1797	NA	–	–	4.26
BPercC4	C_4 proportion	No extinction	−234.83	473.81	0.2396	−0.0072	–	–	4.52
BConstDPercC4	Constant	C_4 proportion	−234.06	474.41	0.1963	NA	0.3638	−0.0958	5.12
BTempDConst	Temperature	Constant	−234.17	474.62	0.1254	0.083	0	–	5.33
BTime	Time	No extinction	−235.67	475.49	0.1865	−0.0072	–	–	6.2
BDConst	Constant	Constant	−235.75	475.63	0.1796	NA	0	–	6.34
BPercC4DConst	C_4 proportion	Constant	−234.83	475.96	0.2396	−0.0072	0	–	6.67
BDTemp	Temperature	Temperature	−234.17	476.82	0.1255	0.0829	0	0.0156	7.53
BTimeDConst	Time	Constant	−235.67	477.63	0.1864	−0.0071	0	–	8.34
BConstDTime	Constant	Time	−235.75	477.78	0.1797	NA	0	−0.0499	8.49
BConstDElev	Constant	Elevation	−235.75	477.79	0.1797	NA	0.0809	−0.0781	8.5
BConstDTemp	Constant	Temperature	−235.75	477.79	0.1796	NA	0	−0.0016	8.5
BDTime	Time	Time	−235.67	479.83	0.1865	−0.0072	0	0.0259	10.54
BDElev	Elevation	Elevation	−236.44	481.36	0.2674	−0.0005	0	0.0022	12.07

phylogenetic reconstruction and dating had a length of between 509 and 4796 bp. Their best substitution models are listed in [Supplementary Data Table S2](#).

Phylogeny

Among the six independent MCMC runs with a Yule tree prior, only one fully converged to a likelihood of -399 351.6164 after discarding 14 % of burn-in (ESS for all the

parameters >200 after discarding the burn-in). The other chains were converging toward a slightly higher likelihood value, but the ESS values for several loci, for the prior and for the Yule model were below 150. After discarding the burn-in, the MCC tree was estimated from 8601 posterior trees. All the nodes in the MCC tree show strong support with all the nodes having a PP of 1, except for two nodes having a PP > 0.9 (Fig. 2). All the genera were retrieved as monophyletic.

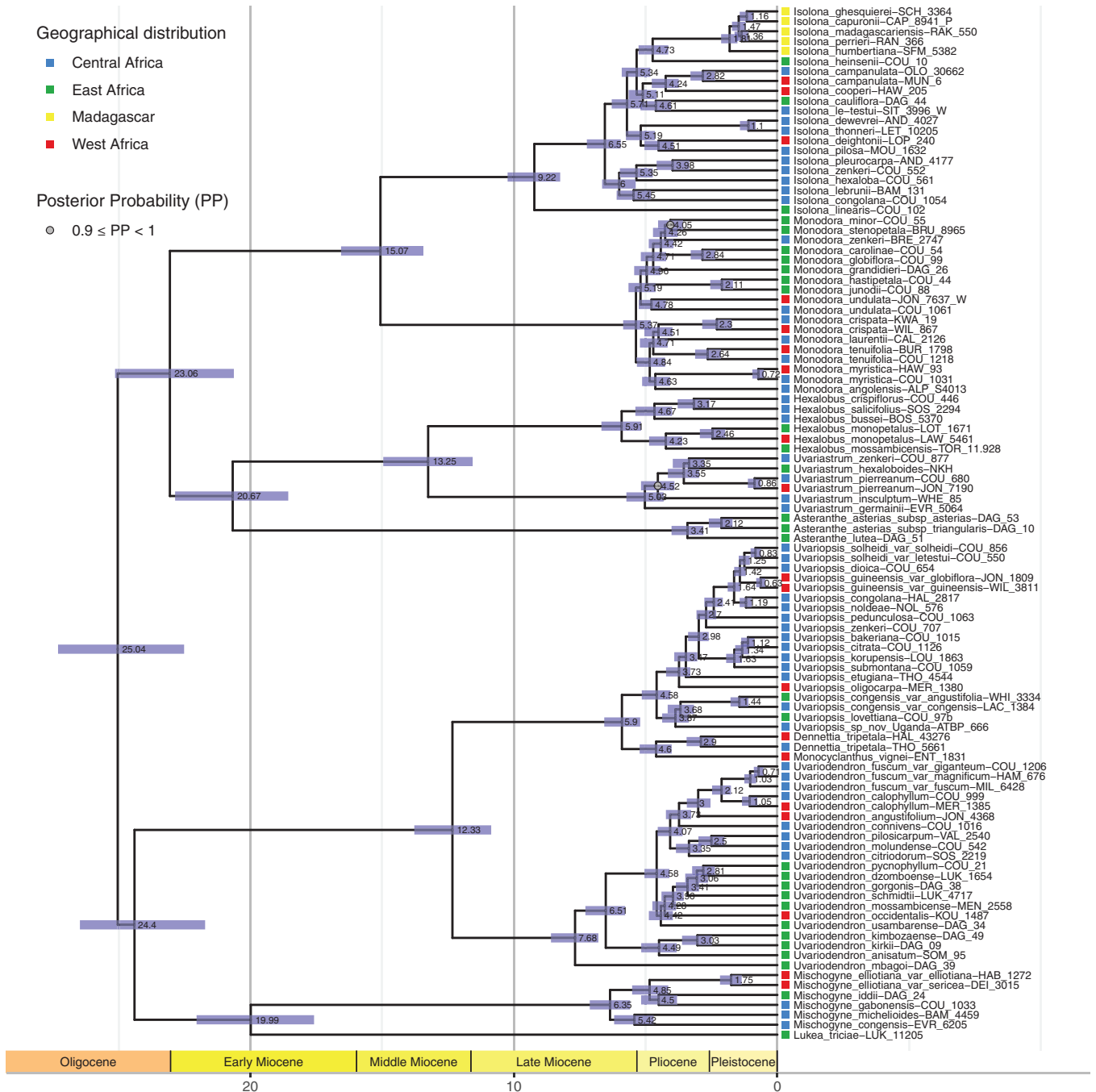


FIG. 2. Phylogenetic tree of the *Monodoreae* specimens, as pruned from the maximum credibility clade tree estimated from 8601 posterior trees inferred based on 32 nuclear loci with uncorrelated molecular clock and fossil calibration in BEAST. Values at nodes indicate the mean age from the posterior probability density, and the blue bar indicates the 95 % highest posterior density interval of the age. All nodes received a posterior probability of 1 except for those indicated by a grey circle. The colour square at the tip indicates the geographical origin of the specimen. Colours follow Fig. 1.

The mean age of the divergence between *Eupomatia* (outgroup) and the Annonaceae (i.e. the crown node of Magnoliineae) is estimated in the Early Cretaceous at 110.68 Ma (95 % HPD: 105.53–112.60 Ma). The crown node of Annonaceae is estimated in the Late Cretaceous at 89.87 Ma (95 % HPD: 89.00–92.55 Ma) (Supplementary Data Fig. S1). Although the distribution probabilities of the calibration points set on these nodes were broad uniforms, the age estimates for the crown node of *Monodoreae* and the crown node of Annonaceae respectively converged to the lower and upper bounds of the prior distribution. This indicates that the data contain enough information to overcome the lack of precise information of such wide priors. The age of the *Monodoreae* tribe is estimated in the late Oligocene at 25.07 Ma (95 % HPD: 22.52–27.30 Ma) (Fig. 2).

Biogeographical events

DEC analysis estimated the rate of ‘dispersal’ (range expansion) to 0.039 events/lineage/Myr and the rate of ‘extinction’ (range contraction) to 0.008. East Africa was identified as the most likely geographical origin of the *Monodoreae* (Fig. 3), as well as for most of the ancestral nodes until ~15 Ma. The ancestral range of *Hexalobus*, *Isolona*, *Mischogyne*, *Monodora* and *Uvariopsis* was probably widespread (Centre-East or West-Centre-East), the ancestral range of *Asteranthe*, *Lukea* and *Uvariadendron* was probably East Africa, while the ancestral range of *Uvariastrum* was probably Central Africa. Between the origin and ~13.5 Ma, the range of the *Monodoreae* expanded, and from ~13.5 to 6.5 Ma the range of some taxa contracted while the range of some other taxa possibly expanded (Fig. 4). From the late Miocene (~6.5 Ma), the *Monodoreae* underwent several synchronous range expansion events, range contraction events and vicariance events. Within *Monodoreae*, a single dispersal event occurred from East Africa to Madagascar in the genus *Isolona* dated between 5.27 and 4.14 Ma. This led to a founder event followed by a small radiation with five known Malagasy species (Fig. 3). Interestingly, the DEC model retrieved this divergence as a vicariance event (Fig. 3). However, as Madagascar had already separated from mainland Africa, it seems unlikely that the ancestor (node 153, Supplementary Data Fig. S1) was distributed in both East Africa and Madagascar. We thus interpret this event as a founder event (Fig. 4).

Diversification analyses

Branch- and clade-specific diversification rates. The three methods used in our study identified to various degrees changes in the speciation and extinction rates across *Monodoreae* and its genera. Nevertheless, BAMM did not detect any significant diversification rate shifts across the phylogeny (Supplementary Data Figs S5 and S6). ClADS inferred low speciation rates in the species-poor (five or fewer species) genera *Asteranthe*, *Hexalobus*, *Lukea*, *Mischogyne* and *Uvariastrum*, and relatively high speciation rates in one of the most diverse genera *Uvariopsis* (Fig. 5). RevBayes estimated higher speciation rates around the crown of the genera *Isolona*, *Monodora*, *Uvariadendron* and *Uvariopsis* (Fig. S3a). The variation of the speciation rate estimated by BAMM was very low, from

0.17 events/lineage/Myr around the root of the phylogeny to 0.2 events/lineage/Myr in the genus *Uvariopsis* (Fig. S4a). These three methods estimated very low extinction rates (<0.03 events/lineage/Myr; Figs S2, S3b and S4b). The three methods have also in common a higher diversification rate in the genus *Uvariopsis*.

Tree-wide diversification rates. Even when using different priors on the survival probability of a sudden extinction event, the different CoMET analyses return similar results (Supplementary Data Figs S7–S16). CoMET found the speciation rate to vary through time: speciation is rather constant at around ~0.2 events/lineage/Myr until ~7 Ma, then increases to around 0.35 events/lineage/Myr between 6.5 and 4 Ma, and finally drops after 4 Ma to below 0.15 events/lineage/Myr (Fig. 6), which corresponds to the detected shifts (see below). The extinction rate is inferred to be rather low and constant through the history of the tribe (Figs S7–S16). CoMET detected a speciation rate shift increase with substantial ($2\ln\text{BF} > 2$) to strong ($2\ln\text{BF} > 6$) support between 6.5 and 7 Ma, followed by a speciation rate shift decrease between 2.5 and 4.25 Ma with substantial support, and a final shift towards even lower speciation rates around 1 Ma with strong support (Fig. 6). CoMET also identified several extinction events with substantial support in the late Miocene (between 10 and 6.5 Ma), with strong support between 6 and 6.25 Ma when the survival probability was <10 % (Fig. 6).

Paleoenvironmental birth–death models. The environmental birth–death model with the lowest AICc score is the BDPerc4 model (four parameters), which is a model with speciation and extinction rates varying exponentially with the proportion of C_4 plants through time (Table 1). However, the estimated parameters for this model are unrealistic as the inferred diversification rate is negative (i.e. extinction rate higher than speciation rate) at the beginning of the clade’s history, which is biologically implausible. The second-best model is the BElev model (two parameters), which is a model with speciation rate varying with mean elevation in tropical Africa through time and no extinction (Table 1; Fig. 7). Note that the difference of AICc between BElev and BElevDConst (speciation varying with elevation through time and constant extinction) is low, but these two models are very similar as the constant extinction rate estimated for BElevDConst is 0.005 events/lineage/Myr (Table 1).

DISCUSSION

In this study we generated a near complete species-level dated phylogenomic tree for a diverse rain forest-restricted clade of pan-African and Madagascar trees. Using this framework, we tested several hypotheses linked to the biogeography and diversification history of rain forests across the continent throughout the Miocene (last 23 Myr). We used BEAST to co-estimate the phylogeny and the divergence times, based on a subsample of the molecular markers available (32 most clock-like markers). The resulting phylogenetic tree is topologically very similar to the one obtained using the full set of molecular markers except for some nodes (mainly in *Isolona*, *Monodora* and *Uvariastrum*) for which phylogenetic conflict was inferred

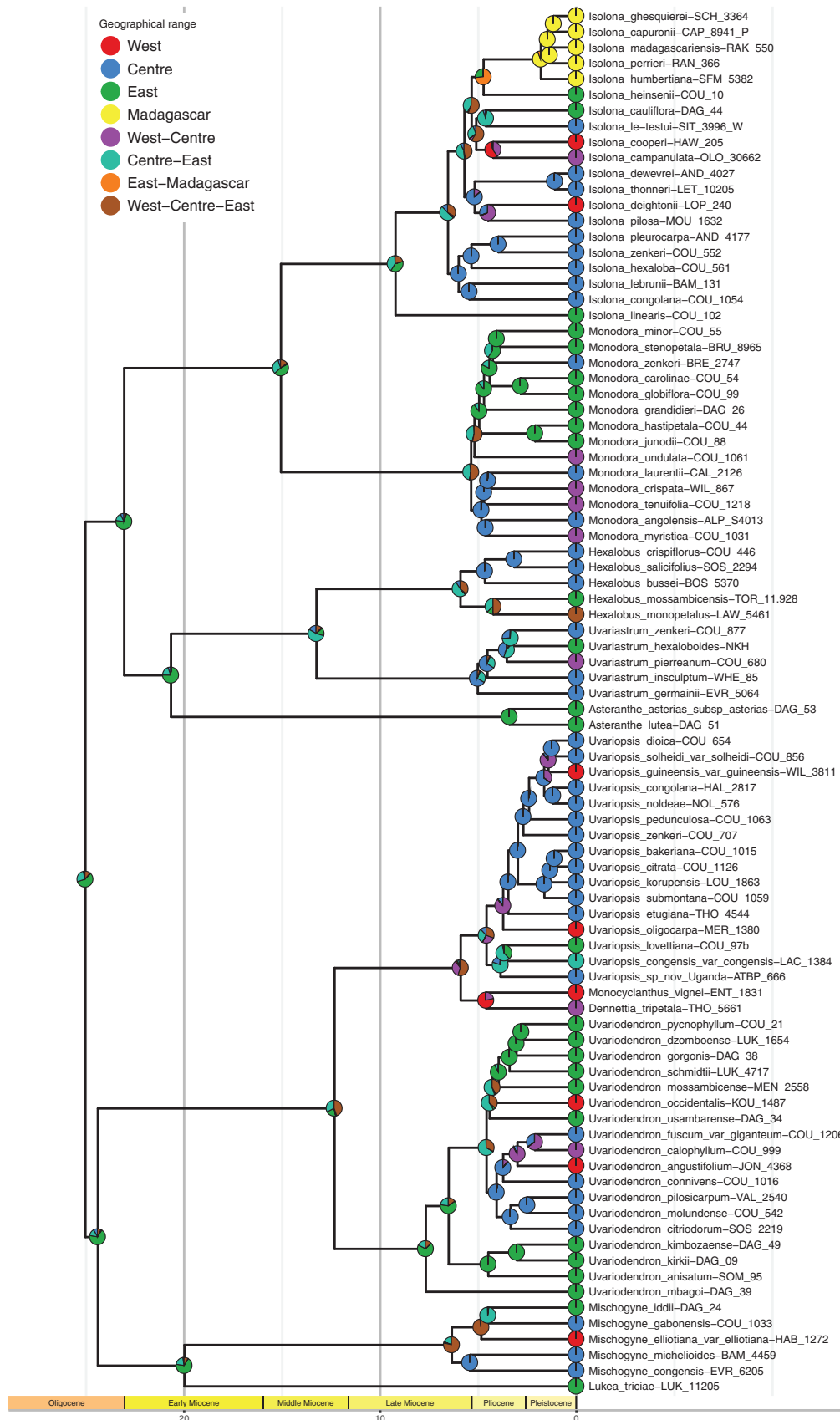


FIG. 3. Phylogenetic tree of *Monodoreae* species, as pruned from the maximum credibility clade tested from 8601 posterior trees inferred based on 32 nuclear loci with uncorrelated molecular clock and fossil calibration in BEAST, with present-day (next to names) and ancestral ranges (pies at the internal nodes) reconstructed using the dispersal-extinction-cladogenesis (DEC) analysis implemented in BioGeoBEARS. The relative proportions of the coloured slices in the pies are proportional to the likelihood of each state.

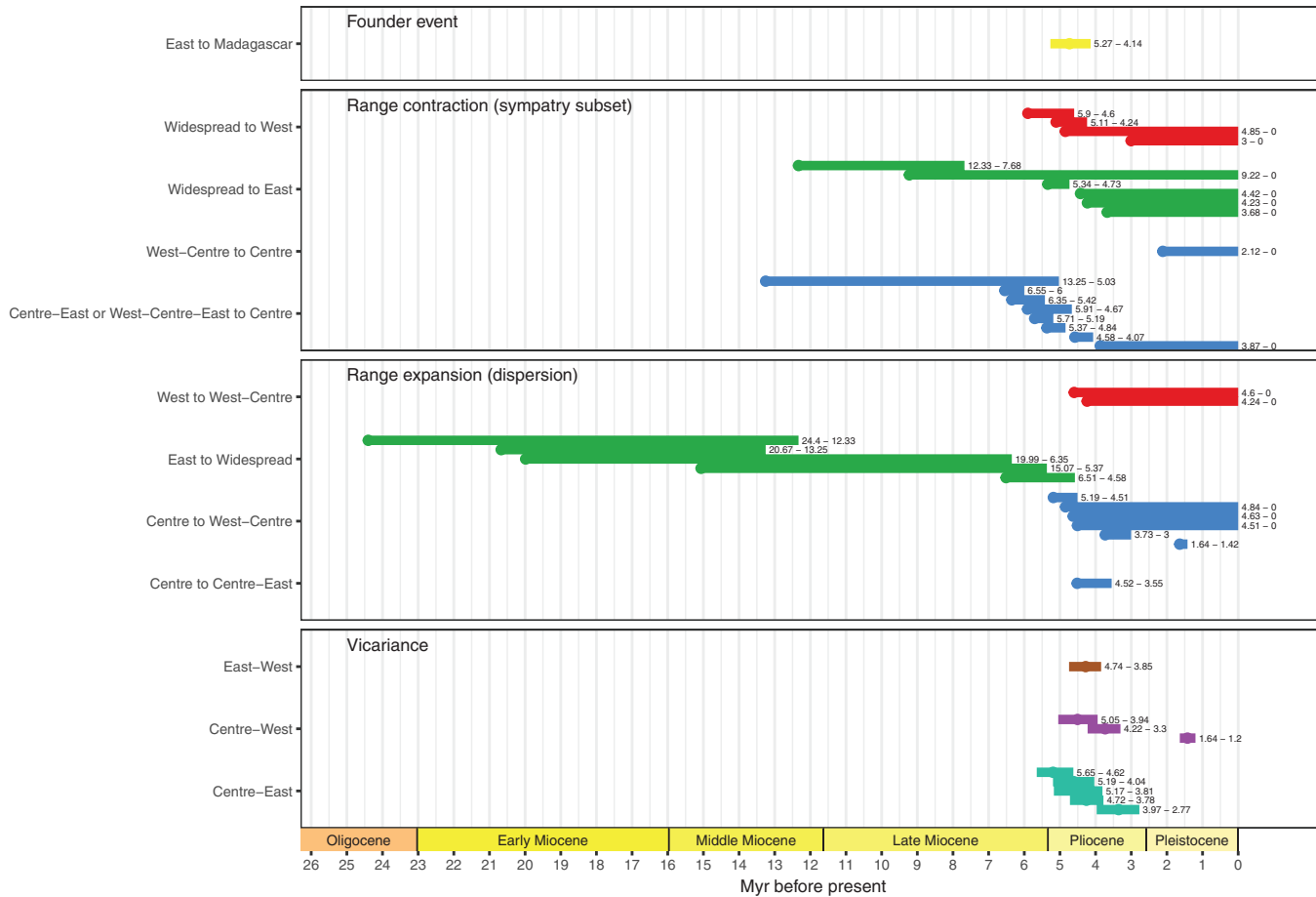


FIG. 4. Chronological time frame of the biogeographical events as interpreted from the dispersal–extinction–cladogenesis (DEC) model. The founder event and vicariance events occurred at nodes of the tree in Fig. 3: the dot and horizontal bar represent the mean age and 95 % highest posterior density interval of the age of the node, respectively. Range contraction (RC) and range expansion (RE) events occurred along branches connecting two nodes: the dot represents the mean age of the widespread (RC) or endemic (RE) ancestral node, and the horizontal bar extends toward the mean age of the endemic (RC) or widespread (RE) daughter node. Colours follow the DEC ranges (see Fig. 3) and have different meaning depending on the event: for founder events, it is the colour of the range after the founder event; for range contraction, it is the colour of the endemic range after range contraction; for range expansion, it is the colour of the endemic range before range expansion; and for vicariance, it is the colour of the widespread range before the vicariance event. Labels on the y-axis indicate the direction of the event (e.g. range expansion from East to Widespread). ‘Widespread’ includes all the widespread ranges (West-Centre, Centre-East or West-Centre-East). See Material and Methods for the details of the events.

using both concatenation and gene tree approaches (Dagallier *et al.*, in press). Reticulate processes of evolution might occur at these nodes, and the selection of only 32 loci for the molecular dating might increase the bias towards one or the other topology. One notable difference is the position of *Monodora minor*, which was inferred as sister to the genus with strong support using the full dataset (Dagallier, 2021; Dagallier *et al.*, in press) but is recovered nested within the genus with moderate support in this 32-marker dataset using BEAST (Fig. 2).

East African origin and biogeography of *Monodoreae*

Our biogeographical analysis inferred East Africa as the most likely ancestral area for the tribe (Fig. 3). Indeed, the East African restricted genera *Asteranthe* or *Lukea* are recovered as sister to the more widely distributed clades. At the genus level, East African endemic species are generally recovered as sister to the rest of the genus (*Isolona linearis*; *Uvariadendron mbagoi*; *Monodora minor*, see above for the last), although not always

(*Uvariopsis*). This scenario contrasts with other TRF groups inferred to have originated in Central Africa before dispersing to East Africa (e.g. Davis *et al.*, 2002; Brée *et al.*, 2020; Aduse-Poku *et al.*, 2021). Interestingly, within Annonaceae, several other East African endemic genera are recovered as sister to different tribes such as *Mkilua fragrans*, sister to the rest of Bocageae (Couvreur *et al.*, 2011a), and the two monotypic endemic genera *Sanrafaelia* and *Ophrypetalum*, sister to the diverse palaeotropical tribe Uvarieae (Dagallier, 2021; Dagallier *et al.*, in press). East African rain forests are thus not only important in terms of species diversity and endemism (Couvreur *et al.*, 2006), but could also potentially contain a unique and old evolutionary history within Annonaceae, stressing their importance for conservation.

The most recent common ancestor of extant *Monodoreae* (crown node) is dated to 25 Ma, during the late Oligocene (Fig. 2). Initially, it was suggested that *Monodoreae* originated just before the Eocene–Oligocene Transition (EOT, 33.9 Ma), but this was based on plastid markers that included the monotypic

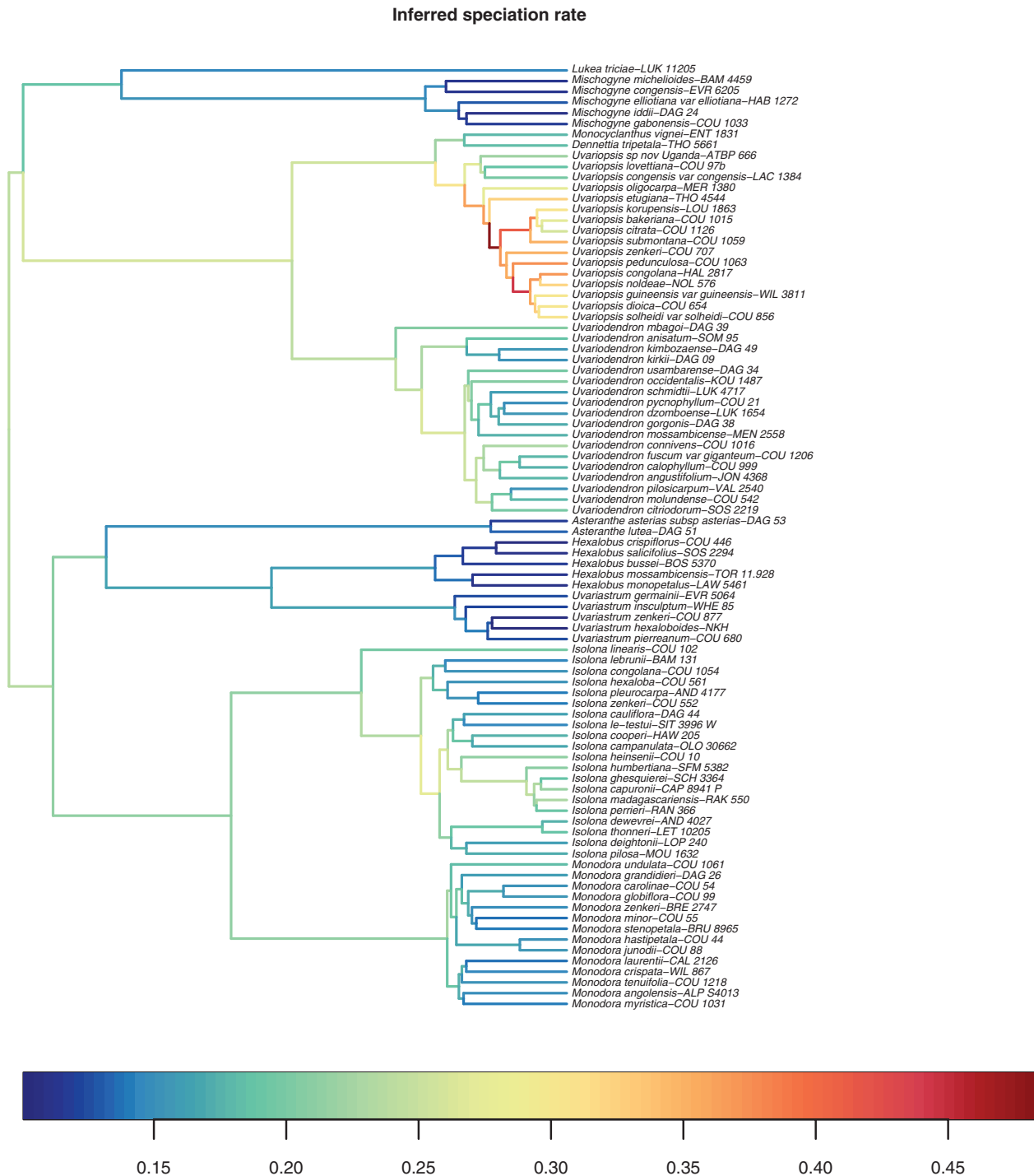


FIG. 5. Species-specific speciation rates through time of Monodoreae estimated using ClaDS (events per million years).

genera *Sanrafaelia* and *Ophrypetalum* in Monodoreae (Couvreur *et al.*, 2008; Chatrou *et al.*, 2012). Based on the analyses of hundreds of nuclear markers both genera are now recovered as sister to tribe Uvarieae and have been transferred to their own tribe: Ophrypetaleae (Couvreur *et al.*, 2019; Dagallier, 2021; Dagallier *et al.*, in press), leading to a 7-Myr younger crown node age for Monodoreae. The late Oligocene (29–24 Ma) was a time of relatively favourable conditions for TRFs, re-expanding

after the EOT crisis (Couvreur *et al.*, 2021). Although the interpretation of East African ecosystems at that time is complex (Jacobs *et al.*, 2010; Linder, 2017), TRF-like vegetation is clearly documented in northern Ethiopia (Jacobs *et al.*, 2005, 2010; Bonnefille, 2010; Pan, 2010; Currano *et al.*, 2011) and in northern Kenya as mosaics of TRFs and semi-deciduous forests (Vincens *et al.*, 2006). The inferred age of Monodoreae also fits well with the origin of several other animal TRF clades,

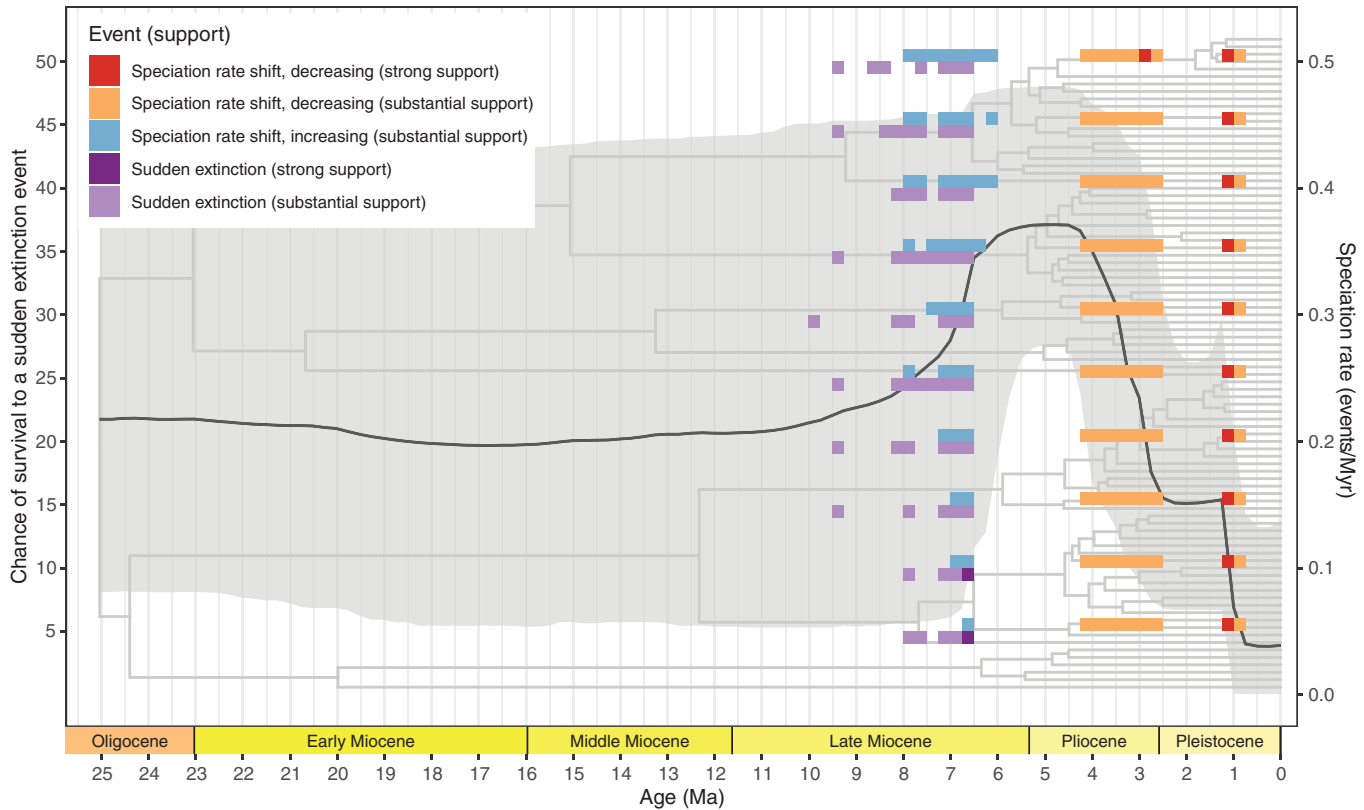


Fig. 6. Summary of speciation rate shifts and sudden extinction (ME) events at each time slice in the CoMET analysis, with the priors on the chance of survival to a sudden extinction event (ME) ranging from 5 to 50 % (Supplementary Data Figs S7–S16). Strong support indicates $2\ln\text{BF} > 6$, and substantial support indicates $2\ln\text{BF} > 2$. Black line represents the speciation rate and grey shading its 95 % credibility interval, both averaged from all the CoMET analyses (Figs S7–S16).

underlying the importance of the late Oligocene in the origin of African rain forest biodiversity (Couvreur *et al.*, 2021).

From East Africa, our biogeographical analysis suggests several range expansions of *Monodoreae* into Central Africa becoming widespread during the early to middle Miocene (~24–13.5 Ma) (Figs 3 and 4, range expansion, green). Given the low potential for long-distance dispersal of this tribe, our results support the hypothesis of important TRF East/Central connections possibly via the existence of a continuous pan-African rain forest (Couvreur *et al.*, 2021; but see Linder, 2017 for a counter argument about the existence of a pan-African forest, and below). Indeed, this coincides with the warmer climate of the MMCO (~17–14.7 Ma) during which the TRF was suggested to occur from coast to coast (Morley, 2000, 2011; Couvreur *et al.*, 2021). It is during the early Miocene (~20–21 Ma) that the genera *Asteranthe* and *Lukea* originated (Fig. 3). These genera are species-poor (two species each) and are endemic to East African coastal and mountain forests (Verdcourt, 1971; Vollesen, 1980; Cheek *et al.*, 2022). Such long-term persistence of clades originating in the Oligocene–Miocene has also been documented in plants and animals (Tolley *et al.*, 2011; Dimitrov *et al.*, 2012; Loader *et al.*, 2014; Couvreur *et al.*, 2021), and is associated with potential climate stability of the region in the East African mountains region (Lovett *et al.*, 2005; Finch *et al.*, 2009). The divergence between *Asteranthe* and the clade *Hexalobus–Uvariastrum* was interpreted as a vicariance event at ~16.8 Ma by Couvreur *et al.* (2008). Here, with full taxon sampling of these genera, we rather estimate a

range expansion from the East to East-Centre ~20.7 Ma with long-term persistence of the genus *Asteranthe* in the East. This period still coincides with warmer and wetter climates across Africa, even though the existence of a continuous TRF between East and West Africa remains debated (Jacobs *et al.*, 2010; Linder, 2017; Couvreur *et al.*, 2021).

Just after the MMCO, during the MMCT (~15–13 Ma), global temperatures and $p\text{CO}_2$ dropped (Westerhold *et al.*, 2020) leading to the expansion of open grasslands across Africa and contraction of TRF (Jacobs, 2004; Plana, 2004; Linder, 2017; Couvreur *et al.*, 2021). Previous molecular studies postulated vicariance events in TRF-restricted clades before the MMCT, supporting the contraction of the TRF during the MMCT (Couvreur *et al.*, 2008; Dimitrov *et al.*, 2012; Menegon *et al.*, 2014; Brée *et al.*, 2020). However, in *Monodoreae*, we did not find evidence of vicariance (i.e. splitting of one species into two) before 6 Ma (Fig. 4). Rather, our results support a range contraction scenario (i.e. the disappearance of a species from part of its past range) from ~13.5 to 6.5 Ma (Fig. 4), leading to the origins of *Uvariadendron* in East Africa, *Uvariastrum* in Central Africa, and corresponding to the divergence between the East African species *Isolona linearis* and the rest of *Isolona* (Fig. 3). Even if these clades evolved in isolation, and would support a contraction of the TRF at that time, their sister clades are inferred as being widespread (i.e. distributed across both East and Central Africa, Fig. 3). Moreover, possible range expansions also continued between ~13.5 and 6.5 Ma (Fig. 4). Overall, these results support the idea that the East and Central

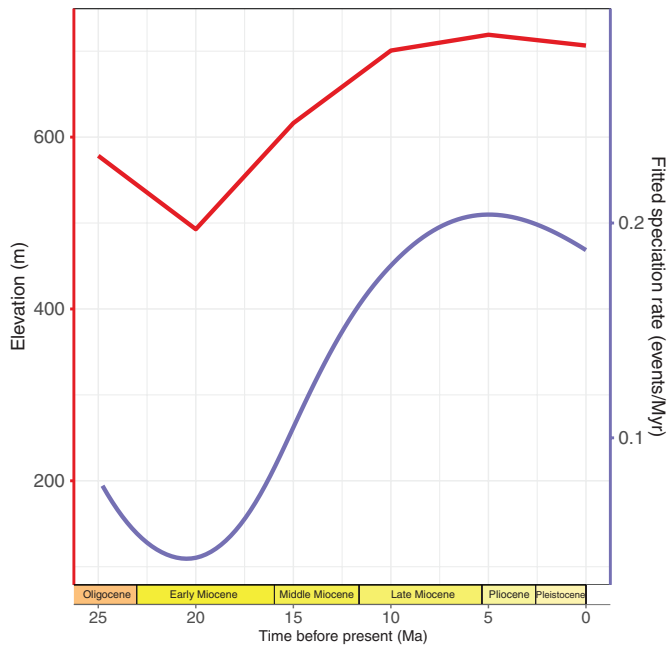


FIG. 7. Clade-independent speciation rate through time of Monodoreae, as estimated in RPANDA with the speciation rate varying exponentially with the mean elevation of tropical Africa through time (BElev model, Table 1).

African TRFs might have been more connected than previously suggested after the MMCT. Indeed, as noted by Jacobs *et al.* (2010), numerous palaeofloras of the middle Miocene of East Africa document the presence of taxa sharing affinities with both wet and dry forests of Central and West Africa. A striking example is that of Baringo in the Ngorora Formation in the East African Rift valley (west Kenya; ~12.2 Ma), inferred as being a moist to wet forest containing several tropical plant lineages, including Annonaceae, and several taxa were suggested to have affinities with modern West African species (Jacobs *et al.*, 2010). Also, as the Monodoreae experienced sudden extinction in the late Miocene (see below), we might miss the ancestral ranges of the extinct (and unknown) species, which may overshadow the signal inferred by DEC between two nodes separated by a long branch.

From the late Miocene and during the Pliocene (6.5–2 Ma), the biogeographical history of the Monodoreae increases in complexity. First, most of the extant Monodoreae species diverged during this time interval (Figs 2 and 3) supporting evidence of the importance of this period for the origin of African biodiversity (Voelker *et al.*, 2010; Couvreur *et al.*, 2021). Second, our biogeographical analysis resulted in numerous simultaneous range expansions, contractions and vicariance events (Fig. 4). This suggests that if TRF fragmentation events occurred, they were not strong enough to affect the whole tribe. Instead, the TRF blocks were probably connected during the early Pliocene, as previously suggested based on a palaeo-vegetation record (Morley, 2000), either as a continuous forest block (Fer *et al.*, 2017) or via forested corridors between East and Centre-West Africa (Joordens *et al.*, 2019). Thus, the late Miocene and Pliocene divergences in the Monodoreae might be explained by species-specific or region-specific mechanisms.

Although most species of Monodoreae are restricted to rain forests, a few isolated species have adapted to dry conditions. Two sister species, *Hexalobus monopetalus* and *H. mossambicensis*, are more dry-adapted than the other *Hexalobus* species distributed in Central Africa (Botermans *et al.*, 2011). *Hexalobus monopetalus* has the typical savanna distribution all around the Guineo-Congolian region (Botermans *et al.*, 2011) like other savanna species (Lehmann *et al.*, 2011; Gonçalves *et al.*, 2021). In addition, *Monodora stenopetala* (Couvreur, 2009) and *Uvariastrum hexaloboides* (Couvreur, 2014) are also reported to be dry-adapted, both occurring in woodlands or dense thickets of southern East Africa. These species, shifting from a forested and wetter to a drier and more open habitat, were estimated to have originated during the late Miocene between 6 and 3 Ma (Fig. 2). These three independent habitat shifts followed by little or no speciation contrast with other plant clades for which multiple shifts into drier habitats followed by speciation have been documented during the late Miocene, such as in the African Melastomataceae (Veranso-Libalah *et al.*, 2018), Cucurbitaceae (Holstein and Renner, 2011), Fabaceae (Bouchenak-Khelladi *et al.*, 2010; Tosso *et al.*, 2018) and Sapotaceae (Armstrong *et al.*, 2014). This supports the view that Annonaceae show little ecological capacity to diversify in drier or arid conditions in Africa in line with previous results (Couvreur *et al.*, 2011b).

Several Monodoreae species span both West and Centre TRF blocks (Figs 2 and 3). The Dahomey Gap (DG) located in Benin and Togo mediates the connection between the West and the Central African forests blocks (Droissart *et al.*, 2018). The DG was suggested to be dominated by open vegetation during most of the late Quaternary, from ~1.05 Ma (Demenou *et al.*, 2018), and became forested during the mid-Holocene (~8000–4000 years before the present), before being dominated again by open vegetation until the present due to climatic variations (Salzmann and Hoelzmann, 2005). These vegetation changes had an impact in the intraspecific genetic structure of many forest tree species (Duminil *et al.*, 2015; Demenou *et al.*, 2018, 2020; Lompo *et al.*, 2018). In this study, we dated the intraspecific divergence times of eight species co-occurring west and east of the DG (one individual per side sampled). For three of these species (*Monodora myristica*, *Uvariastrum pierreanum* and *Uvariadendron calophyllum*), divergence times were estimated to the late Quaternary (i.e. after 1.05 Ma) (Fig. 2). In addition, no *interspecific* vicariance events between West and Centre species were inferred during this period (Figs 3 and 4), suggesting that the presence of the DG acted as a barrier only for genetic differentiation within species as is generally reported (Couvreur *et al.*, 2021). We also inferred intraspecific divergence times prior to 1.05 Ma spanning 6.57–1.20 Ma associated with inter- and intraspecific vicariance and range expansion events between the West and Central TRF blocks (Figs 2–4). This result agrees well with the scenario of multiple expansion and retractions of savannah vegetation in West Africa, connecting and disconnecting rain forests between West and Central Africa throughout the last 7 Myr (Bonnieffille, 2010; Jacobs *et al.*, 2010). In particular, the climatic variations in the Pliocene and the early Pleistocene (mainly glacial and interglacial cycles, Couvreur *et al.*, 2021) triggered strong isolations in some populations, leading to splits between West and Central African species (e.g. origin of *Isolona deightonii*, *Uvariopsis*

guineensis or *Uvariopsis oligocarpa*), but also seem to have allowed the re-connection of the populations of some species distributed in both West and Central Africa (e.g. *Monodora undulata*, *Dennettia tripetala*). A similar pattern with both inter- and intraspecific divergence between West and Centre Forest blocks has been observed during the Pliocene and Pleistocene in the bird genera *Bleda* and *Criniger* (Huntley and Voelker, 2016; Huntley et al., 2018).

Madagascar broke apart from Africa in the Early Cretaceous (more than 100 Ma; Kocsis & Scotese, 2021) and the shortest distance today separating the African coast to Madagascar is ~400 km (Rabinowitz and Woods, 2006). Similar recent splits between Malagasy clades and continental relatives have been inferred in animals and plants (Renner, 2004; Rabinowitz and Woods, 2006; Yoder and Nowak, 2006; Tolley et al., 2013), including other Annonaceae (Thomas et al., 2015; Chen et al., 2019), and have generally been explained by long-distance dispersal (LDD). Small vertebrates and invertebrates are hypothesized to have drifted on vegetation rafts from continental African rivers with the help of eastwards oceanic currents (Rabinowitz and Woods, 2006; Ali and Huber, 2010). LDD from the continent to Madagascar is likely in wind-dispersed plant species and is also documented in bird-dispersed plant species (Renner, 2004; Yao et al., 2016). *Isolona* is the only *Monodoreae* genus that reached Madagascar. We estimated that this event happened during the early Pliocene between 5.27 and 4.14 Ma followed by a small radiation of five species (Figs 3 and 4). The timing of this dispersal occurs on the more recent timeline of endemic plant lineage origins in Madagascar which span the middle Eocene/Oligocene to the Pleistocene (Buerki et al., 2013; Antonelli et al., 2022). The fruits of *Isolona* are large syncarps probably dispersed by large to medium-bodied primates (Couvreur, 2009), and terrestrial LDD is considered unlikely in this genus (Couvreur et al., 2008). To explain the presence of *Isolona* in Madagascar, we speculate that some propagules (fruits, seeds or seedlings) derived from mainland rivers in East Africa to the ocean and reached Madagascar by drifting via an eastward oceanic current. This is supported by the fact that the sister species to the Malagasy clade is *Isolona heinsenii* endemic to the East African rain forests in Tanzania (Verdcourt, 1971; Couvreur, 2009; Dagallier, 2021; Dagallier et al., in press). Dispersal by drifting to Madagascar is suggested as the main hypothesis for the origin of Malagasy biodiversity (Yoder and Nowak, 2006; Buerki et al., 2013; Antonelli et al., 2022), and has also been suggested in the palaeotropical Annonaceae genus *Uvaria*, for which the African species are also unlikely to disperse across the ocean (Zhou et al., 2012). Although seed survival of *Isolona* (and *Monodoreae* in general) in salt water remains unknown, it is possible that some propagules survived during the crossing, especially if they drifted on rafts of vegetation detached from East Africa (Ali and Huber, 2010). An alternative hypothesis could be that the propagules of an ancestral *Isolona* species reached Madagascar via land bridges linking Africa and Madagascar (e.g. Masters et al., 2021) and allowing different animal migrations, notably at three distinct moments during the Cenozoic, including the Miocene (12–5 Ma). However, viable land bridges across the Mozambique Channel were shown to be very unlikely (Ali and Huber, 2010; see Ali and Hedges, 2022 for a review). In addition, crossing the channel even when the sea level was low is

also improbable, given that the bathymetry is deep, and even a drop of 200 m would only reduce the distance between the continent and Madagascar to 360 km (Rabinowitz and Woods, 2006). Finally, the presence of *Isolona* in Madagascar was used as a counter argument to our assumption of low potential for LDD of *Monodoreae* species (Linder, 2017). However, this successful dispersal event occurred only once throughout the evolutionary history of *Monodoreae* and should thus be viewed as additional proof of the low LDD capacity of the species in this tribe, not the opposite.

Diversification of the *Monodoreae*

Speciation rates for *Monodoreae*, as inferred with CoMET, were relatively stable until the late Miocene some 10 Ma (Fig. 6). The first event detectable with our data was a sudden extinction occurring during the late Miocene between 10 and 6.5 Ma (Fig. 6; Supplementary Data Figs S7–S16). Similarly, Brée et al. (2020) found substantial support in favour of a sudden extinction around the same time, between 8 and 6.5 Ma in the Piptostigmatae, another TRF African Annonaceae tribe, although they do not consider it significant (see fig. 4 in Brée et al., 2020). This pattern has also been retrieved in the African butterfly genus *Bicyclus* for which the forest clade underwent a drop in diversification rate from ~15 Ma (Aduse-Poku et al., 2021). These results are consistent with the late Miocene cooling suggested to have increased aridification across Africa and leading to the expansion of open grasslands (Jacobs, 2004; Uno et al., 2016; Couvreur et al., 2021), although this trend was not homogenous through time or space (Jacobs, 2004; Bonnefille, 2010). This supports growing evidence that the open grasslands in the late Miocene occurred at the expense of the TRFs, which might have experienced drastic and sudden extinction due to the reduction of areas having a suitable warm and wet climate (Morley, 2000, 2011).

Interestingly, using two different methods (CoMET and the environment-dependent diversification model) our results indicate that this sudden extinction event was immediately succeeded by a potential increase in speciation rates dated to have taken place between 6.5 and 4.25 Ma (Figs 6 and 7; Supplementary Data Figs S7–S16). This increase coincided with the early Pliocene which was marked by a renewed warmed climate across Africa (Jacobs et al., 2010; Couvreur et al., 2021). Our biogeographical analysis identifies numerous vicariance events between major regions also dating to the early Pliocene (Fig. 4).

In addition, the model with change of elevation through time best explained the speciation rate with no extinction in *Monodoreae* (BElev model; Fig. 7; Table 1, but see Results). This is, to our knowledge, the first time African elevation change (orogeny) is positively linked to speciation in an African rain forest tree clade. The timing of the orogeny of the East African Rift system is complex (Chorowicz, 2005; Ring et al., 2018; Couvreur et al., 2021), but our results would fit with an active phase of uplift suggested to have occurred along the Western branch around 15–10 Ma (Chorowicz, 2005; Wichura et al., 2015; Ring et al., 2018). The rise of the East African Rift has generally been interpreted as having a negative impact on African rain forest biodiversity leading to precipitation reduction and the drying of the Congo basin for example (Sepulchre

et al., 2006; Sommerfeld et al., 2016). However, rifting in East Africa could have led to the fragmentation or complete genetic isolation of both East and West/Central Forest blocks favouring vicariance (Fig. 4).

Taken together, our results suggest that both aridification and rifting initially had a negative impact on TRF diversity but this was quickly followed by an increase in speciation linked to vicariance. We suggest here a ‘sequential scenario of diversification’ starting with an increased aridification triggering extinction of TRF taxa followed by the fragmentation of rain forests resulting from a reduction in rainfall that subsequently enhanced lagged speciation events resulting from vicariance and improved climate conditions.

Uvariopsis, an outlier in the diversification of *Monodoreae*?

At the clade level, our BMM analyses failed to detect any significant shifts in diversification rates across *Monodoreae* (Supplementary Data Figs S5 and S6). This is in line with previous studies that failed to detect significant diversification shifts either across Annonaceae as a whole (Couvreur et al., 2011a; Erkens et al., 2012) or within the Annonoideae sub-family (which includes *Monodoreae*) (Massoni et al., 2015a), suggesting a rather constant rate of diversification at least at higher taxonomic levels in Annonaceae. Nevertheless, diversification rates in *Monodoreae* are not homogeneous across genera (Fig. 5; Figs S3 and S4), and BMM has been shown in some cases not to detect shifts even though they exist (Rabosky, 2014; Mitchell et al., 2019). All analyses found higher diversification rates in the genus *Uvariopsis* when compared to the other genera. With 20 species (17 described and three undescribed, see Dagallier et al., in press), *Uvariopsis* is one of the most species-rich and youngest genera of the tribe (crown node: median 5.90 Ma, 95 % HPD 5.21–6.57 Ma). Using the methods of moments (Magallón and Sanderson, 2001), that is using species richness and age of the stem node, *Uvariopsis* was identified as one of the fastest diversifying Annonaceae genera under a no extinction hypothesis (Couvreur et al., 2011a). Indeed, all extant species diverged between ~4.5 and 1 Ma, whereas most of the species in the other rich genera [*Isolona* (20 species), *Monodora* (14 species), *Uvarioidendron* (18 species)] diverged between 10 and 4 Ma (Fig. 2). Morphologically, *Uvariopsis* has several features differentiating it from other *Monodoreae*. All but one species are monoecious, that is have separated male (staminate) and female (pistillate) flowers on the same individual (except *U. bisexualis*, not included in this study) and they all present a reduction of the perianth parts (two sepals and three or four petals) when compared to the typical Annonaceae flower (three sepals and 6 petals) (Dagallier, 2021; Dagallier et al., in press). Such an association between monoecy and reduction of perianth parts has been suggested to be an optimization of resource allocation to sex (Jong et al., 2008). Monoecy could be evolutionary advantageous to avoid self-pollination (Pang et al., 2013), but the flowers of most Annonaceae species generally avoid self-pollination with temporal variation in the maturation of stamens and carpels (Pang and Saunders, 2014). Another evolutionary advantage of monoecy is probably conferred by the flexibility in resource allocation to male and female functions (Bertin, 1993). However, recent analyses found unisexual flowers associated with lower diversification

rates than in bisexual flowers and androdioecous flowers at the population level (Xue et al., 2020). Three species of *Uvariopsis* are pollinated by Diptera (Gottsberger et al., 2011; Mertens et al., 2018), which is quite uncommon in Annonaceae (Saunders, 2012). Shifts in pollination syndromes have been suggested to be responsible for shifts in diversification (Valente et al., 2012; Breilkopf et al., 2015; Lagomarsino et al., 2016; Serrano-Serrano et al., 2017). One would be tempted to relate the peculiarities of *Uvariopsis* (monoecy and Diptera pollination) to its higher diversification rates relative to the other *Monodoreae* genera. However, given these characters appeared only once in *Monodoreae*, testing for their influence on diversification rates (e.g. with state-dependent speciation and extinction models; Maddison et al., 2007) could provide spurious inferences (Maddison and FitzJohn, 2015).

CONCLUSION

Our study brings new and more detailed insights into the evolution of TRFs in Africa during the Cenozoic. By focusing on *Monodoreae*, we found that this clade originated in East African TRFs during the late Oligocene (~25 Ma) after the EOT and expanded toward Central/West Africa during the early to middle Miocene, supporting the existence of a pan-African rain forest until ~13.5 Ma. There is no evidence for clear discrete and synchronous vicariance events between forest blocks during the middle Miocene as previously suggested, but instead range contractions that led to speciation support the hypothesis of TRF fragmentation due to aridification in Africa. However, we also inferred clades spanning several forest blocks during the middle Miocene, suggesting that the TRF blocks were more connected than previously thought. The *Monodoreae* probably experienced sudden extinction during the late Miocene, supporting the drastic reduction of the TRFs linked to aridification. This was quickly followed by high speciation rates, suggesting that both the fragmentation and the following re-connection of the TRFs in the early Pliocene stimulated diversification. Such a high diversification was probably associated with the increasing African palaeo-elevation during the late Miocene and Pliocene, supporting the idea that the uplift of East Africa was a factor that promoted diversification.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Fig. S1: Phylogenetic inference of the *Monodoreae* and outgroups. Fig. S2: Extinction rates of *Monodoreae* estimated using ClaDS. Fig. S3: Speciation, extinction and diversification of *Monodoreae* estimated using RevBayes. Fig. S4: Clade-specific speciation, extinction and diversification rates through time of *Monodoreae* estimated using BMM. Fig. S5: Traces of the MCMC run for the BMM analysis. Fig. S6: Posterior probabilities of the number of diversification rate shifts in the *Monodoreae* phylogeny according to BMM. Figs S7–S16: Results of the CoMET analysis, with different priors on the chance of survival to a mass extinction event. Fig. S17: Estimated proportion of C_4 plants in tropical Africa interpolated from Polissar et al. (2019). Table S1: Information on the vouchers used in

this study. Table S2: Length and best substitution model of the 32 loci used in this study.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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