








RESEARCH ARTICLE

Recent and local diversification of Central American understorey palms

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Abstract

Aim: Central America is largely covered by hyperdiverse, yet poorly understood, rain forests. Understorey palms are diverse components of these forests, but little is known about their historical assembly. It is not clear when palms in Central America reached present diversity levels and whether most species arrived from neighbouring regions or evolved locally. We addressed these questions using the most species-rich American palm clades indicative of rain forests. We reconstructed and compared their phylogenomic and biogeographical history with the diversification of 54 other plant lineages, to gain a better understanding of the processes that shaped the assembly of Central American rain forests.

Location: Central America.

Time period: Cretaceous to present.

Major taxa studied: Arecaceae: Arecoideae: Bactridinae, Chamaedoreae, Geonomateae.

Methods: We sampled 218 species through fieldwork and living collections. We sequenced their genomic DNA using target sequence-capture procedures. Using 12 calibration points, we reconstructed dated phylogenies under three approaches (multispecies coalescent, maximum likelihood and Bayesian inference), conducted biogeographical analyses (dispersal–extinction–cladogenesis) and estimated phylogenetic diversity metrics.

Results: Dated phylogenies revealed intense diversification in Central America from 12Ma. Local diversification events were four times more frequent than dispersal events, and we found strong phylogenetic clustering in relationship to Central America.

Main conclusions: Our results suggest that most understorey palm species that characterize the Central American rain forests today evolved locally after repeated

Mathieu Perret and Alexandre Antonelli share last authorship.

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dispersal events, mostly from South America. Understorey palms in Central American rain forests diversified primarily after closure of the Central American Seaway at c. 13 Ma, suggesting that the Great American Biotic Interchange was a major trigger for plant diversification in Central American rain forests. This recent diversification contrasts with the much earlier existence of rain forest palms in neighbouring South America since c. 58 Ma. We found similar timings of diversification in 54 other seed plant lineages, suggesting an unexpectedly recent assembly of the hyperdiverse Central American flora.

KEYWORDS

Arecaceae, biogeography, Central America, diversification, palms, phylogenetic diversity, phylogenomics, target sequence-capture, tropical rain forest

1 | INTRODUCTION

The Central American biota is hyperdiverse, with most of its plant species richness concentrated from Costa Rica to the Chocó Biogeographical Region, in an area considered the most diverse of the top five global centres of plant diversity (Barthlott et al., 2007). Major geological events have taken place in Central America since the Miocene, including land emergence from north to south, ending with the closure of the Isthmus of Panama, volcanism, and flooding of the Nicaraguan depression (Gutiérrez-García & Vázquez-Domínguez, 2013; Montes et al., 2015; and references therein). This changing landscape is likely to have impacted the diversification of its flora, owing to new niches becoming available and the eventual meeting of the North and South American biotas. Despite the potential of Central America for investigation of the interplay between biological evolution and a dynamic geological history, the biogeography of this region has received little attention in comparison to other Neotropical regions, such as the Andes (e.g., Hazzi et al., 2018) and Amazonia (e.g., Antonelli et al., 2018). In particular, little is known about the evolutionary processes that shaped the rich biodiversity observed in Central American tropical rain forests (TRFs) today and its evolutionary response to major landscape and climatic events.

Palms (Arecaceae) are major components of TRFs throughout the Americas (Henderson et al., 1995), where some species are hyperdominant (e.g., ter Steege et al., 2013). Across Central America, the palm family presents a high species richness, with 219 species reported (Govaerts et al., 2021), and is among the most abundant

plant families (e.g., Condit et al., 2019; Gentry, 1982). Most species in Central America belong to three lineages of subfamily Arecoideae: subtribe Bactridinae (166 species), tribe Chamaedoreae (123 species) and tribe Geonomateae (99 species) (global number of species per clade according to Roncal et al., 2013; Figure 1). These are associated with TRFs because most species occur in the dark, humid and warm understorey of these ecosystems (Henderson et al., 1995). Molecular studies (Baker & Couvreur, 2013; see Supporting Information Appendix S1, Figure S1.1) and the fossil record from northern South America (Gomez-Navarro et al., 2009) indicate that ancestors of these three lineages originated and diversified in South America from the Palaeocene, subsequently reaching Central and North America, and only *Hyophorbe* (in tribe Chamaedoreae) expanded outside the Americas and colonized the Mascarene Islands (Baker & Couvreur, 2013). Each of these independently evolving and monophyletic groups (Baker et al., 2009) comprises species distributed across the Neotropics, mostly in Central and South America, that coexist in TRFs of Central America, where many of them are endemic (15% of Bactridinae species, 76% of Chamaedoreae species and 31% of Geonomateae species; Govaerts et al., 2021). Although the distribution and systematics of these clades have been studied previously (e.g., Henderson, 2000, 2011; Hodel, 1992), how their diversity was shaped remains poorly understood.

Two essential questions remain unanswered (Table 1). Firstly, how old is the high understorey palm diversity in Central America? Our null hypothesis (Table 1, H₁₀) is that palm diversity in Central America assembled mainly during the Eocene. The fossil record could

FIGURE 1 Phylogeny of Central American palms (Arecaceae), displaying geographical range evolution. Branch tips represent extant species sampled for this study. Photographs illustrating the understorey growth habit and the morphology of tribe Chamaedoreae (top right), tribe Geonomateae (middle right) and subtribe Bactridinae (bottom right) are shown at the tips of the tree (credit: Á. Cano). Branches are coloured according to the most probable area occupied by the most recent common ancestor of a given lineage (located where two branches bifurcate; colour codes are indicated in the inset map). Inset palaeomaps show geological reconstructions of Central America at 43 Ma (left) and 8 Ma (right) (Jaramillo, 2018; Matthews et al., 2016), where arrows summarize the dispersal events reconstructed for tribe Chamaedoreae (left) and all Central American radiations (right) around those time periods. Lineage-through-time (LTT) plots of Central American radiating lineages (I–IV), from their initial dispersal to the region until the present, are shown at the bottom of the figure: Black lines represent the LTT described by the Bayesian inference maximum clade credibility tree, and grey lines represent LTTs of 100 samples randomly extracted from the Bayesian analysis. The arrow shows the colonization event of each lineage to Central America

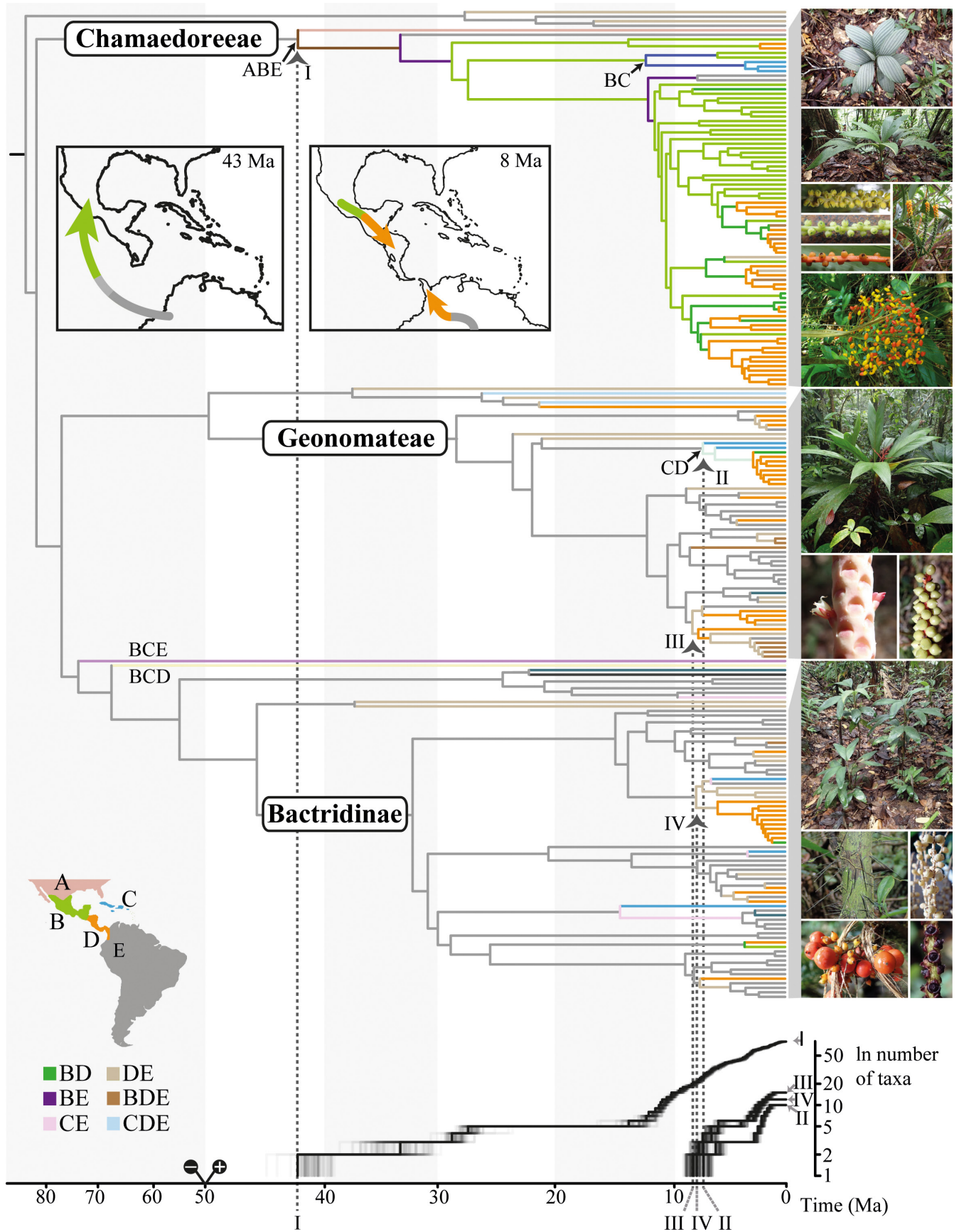


TABLE 1 Questions and hypotheses tested in this study on the historical assembly of understory palms in Central America and their temporal and geographical justifications based on available literature

Question 1	How old is the high understory palm diversity in Central America?
H1₀	High understory palm diversity in Central America assembled mostly during the Eocene
Justification	<ol style="list-style-type: none"> 1. Land was available in northern Central America before the Eocene (Gutiérrez-García & Vázquez-Domínguez, 2013) 2. Molecular studies (Baker & Couvreur, 2013; see Supporting Information Appendix S1, Figure S1.1) and the fossil record (Gomez-Navarro et al., 2009) indicate that some palm lineages were already present in South America from the Palaeocene and were available to colonize the Central American emerging land 3. An Eocene palm fossil, of unknown placement within palms and unknown habitat preferences (e.g., rain forest, coastal environments), has been found in Central America (Herrera et al., 2012)
H1_a	High understory palm diversity in Central America assembled more recently, during the Miocene
Justification	<ol style="list-style-type: none"> 1. High species richness is found in the Miocene palm fossil record from southern Central America (Jaramillo et al., 2014) 2. Some Central American plant lineages have shown recent radiations (e.g., Erkens et al., 2012; Richardson et al., 2001)
Question 2	Did Central America palm species arise locally or did they originate elsewhere and subsequently colonize Central America?
H2₀	A small number of dispersal events from neighbouring areas were followed by intense local diversification
Justification	Local diversification was found to be more important than dispersal for some tropical rain forest Central American radiations (Dexter et al., 2017; Kissling et al., 2012; Moonlight et al., 2015; Perret et al., 2013)
H2_a	Most of the palm diversity in Central America originated elsewhere and subsequently dispersed to Central America
Justification	<ol style="list-style-type: none"> 1. Dispersal is a key process in the diversification of Malpighiaceae in Central America (Willis et al., 2014) 2. Central America is a land bridge that facilitates biotic dispersal between the north and south of America

support this scenario, because it includes an Eocene palm fossil, although of unknown habitat preferences (e.g., rain forest or coastal environments), from what is now the Panamanian Azuero Peninsula (Herrera et al., 2012). Further support for this hypothesis comes from the fact that land was available to be colonized in northern Central America before the Eocene (Gutiérrez-García & Vázquez-Domínguez, 2013) and that phylogenetic (Baker & Couvreur, 2013; see Supporting Information Appendix S1, Figure S1.1) and palaeontological (Gomez-Navarro et al., 2009) studies suggest that palm lineages occurred in South America before the Eocene and were available to colonize Central America. An alternative hypothesis (H1_a) is that high understory palm diversity in Central America assembled more recently, during the Miocene. This is substantiated by the rich Miocene palm fossil record from southern Central America (Jaramillo et al., 2014) and has been shown to be the case in several species-rich Central American plant lineages that represent young radiations (e.g., Erkens et al., 2012; Richardson et al., 2001).

Secondly, did Central American palm species arise locally or did they originate elsewhere and subsequently colonize Central America? Local diversification is suggested to have been more important than dispersal in contributing to species richness of individual Central American plant lineages (Dexter et al., 2017; Kissling et al., 2012; Moonlight et al., 2015; Perret et al., 2013). Therefore, our null hypothesis (Table 1, H2₀) is that a small number of dispersal events from neighbouring areas were followed by intense local diversification. However, other lines of evidence, for species associated with seasonally dry forests (e.g., Willis et al., 2014), support the alternative hypothesis (H2_a) that most species dispersed to Central America from other regions, whereas local diversification occurred less frequently in this important biotic corridor that links the Americas.

Here, we test these alternative hypotheses using a newly assembled palm phylogeny based on genomic data, including intensive sampling in Bactridinae, Chamaedoreae and Geonomateae, and dated using 12 calibration points. We then compare our findings on palms with the diversification of 54 plant lineages belonging to 26 families, to evaluate the extent to which palm diversification could be indicative of the evolutionary processes that drove lineage diversification and endemism in the highly diverse and increasingly threatened forests of Central America.

2 | MATERIALS AND METHODS

2.1 | Sampling, sequencing and bioinformatics

A flowchart summarizing the methods of this study is presented in the Supporting Information (Appendix S1, Figure S1.2). We sampled 237 individuals, representing 218 palm species, in the field (permits SE/P37-13 and SC/P6-14, National Environmental Authority of Panama) and living collections. Leaf tissue was dried in silica gel for DNA extraction and accompanied by reference vouchers deposited in the University of Panama (PMA) and Geneva (G) herbaria (Supporting Information Appendix S1, Table S1.1). Sampling was focused on Bactridinae, Chamaedoreae and Geonomateae (64, 69 and 48 species sampled, respectively), representing all their genera. Other palm lineages (37 species, belonging to 15 tribes and four out of five subfamilies) were sampled to provide a phylogenetic backbone (Supporting Information Appendix S1, Figure S1.1) and for dating purposes, given their associated fossils (Supporting Information Appendix S1, Table S1.2).

Genomic DNA were extracted using NucleoSpin Plant II (Machery-Nagle), following the procedure described by Cano

et al. (2018). DNA sonication, library preparation and hybridization procedures followed de Sousa et al. (2014). Four hundred nanograms of DNA per sample was used to construct libraries with the NEXTflex DNA Rapid Sequencing Kit and NEXTflex DNA Barcodes (BIOO Scientific, Austin, TX, USA). Agencourt AMPure XP magnetic beads (Beckman Coulter) were used for fragment size selection to exclude fragments <400 and >600bp. A PCR run of 14 cycles was performed, following the manufacturer's instructions. PCR purification was done with the QIAquick Purification kit (Qiagen, Hilden, Germany). Sequence capture targeted 837 exons from 176 nuclear genes (Heyduk et al., 2015). Captured libraries were sequenced by the Swedish Science for Life Laboratory, on a MiSeq v.3 platform from Illumina (San Diego, CA, USA), producing 300bp paired-end reads.

Raw sequences were processed with the SECAPR pipeline (Andermann et al., 2018), applying default settings unless evaluation of the outputs suggested otherwise. SECAPR was developed and tested with the same *Geonoma* sequences used here; therefore, default settings are optimized for the data in the present study. Trimming and filtering of the raw reads was done using TRIMMOMATIC-0.36 (Bolger et al., 2014). The cleanest results (see quality control below) were obtained with a sliding window of size four with quality of 15, cutting 10 bases from the start of a read and the necessary bases at the end of a read to keep read length to a maximum of 260bp, and dropping reads shorter than 100bp. The quality of the samples was determined according to the thresholds defined by FASTQC v.0.11.05 (Andrews, 2010). Clean reads were assembled *de novo* to produce contigs that included introns with the assembler ABYSS (Simpson et al., 2009) using the SECAPR assemble_reads function, discarding contigs that were shorter than 100bp. Using the function find_target_contigs, contigs were blasted against the reference sequences of the targeted loci that were used for bait design.

De novo assembly software, such as ABYSS, is designed to merge homologous reads with little expected read variation into a single contig, but it will produce several separate contigs for regions with high read variation, such as loci affected by paralogy. Although only target regions without signs of paralogy were selected during bait design, as an additional precaution to avoid such regions we discarded all loci that produced multiple contig matches in any of the samples. Multiple sequence alignments for each non-paralogous targeted locus were built with the align_sequences function, using the contigs of all samples that could be extracted in this manner. Several of the resulting alignments showed high degrees of incompleteness (i.e., they were lacking contig sequences for several samples). Given that the blast approach is sensitive to the amount of sequence variation between the reference library and the assembled contigs, the limited contig yield for some of the target loci is likely to be a result of the evolutionary distance between the reference taxa from which the bait sequences were compiled and the samples analysed in this study. To produce a more appropriate and taxonomically more targeted reference library, we generated lineage-specific references from the contig alignments produced in the previous step.

To do so, we divided each alignment by monophyletic palm lineages formally recognized by Baker et al. (2009): Attaleinae, Bactridinae, Calamoideae, Ceroxyloideae, Chamaedoreae, Coryphoideae, Elaeidinae, Euterpeae, Geonomateae, Iriarteeae, Manicarieae, Reinhardtiae and Roystoneae. We generated a consensus sequence for each locus from the retrieved contigs of each lineage, which we then used as new references, onto which the clean reads were mapped. This was performed using the BWA mapper (Li & Durbin, 2009) as implemented in the phase_alleles function, setting the minimum seed length to 70. We produced consensus sequences of the mapped reads at each locus, then multiple sequence alignments, using the align_sequences function. In contrast to the first contig alignments, these sequences are, on average, longer and are recovered for more loci for each sample, owing to the specific reference libraries created in the previous step (Andermann et al., 2018).

2.2 | Phylogenetic reconstruction and divergence time estimation

From the 837 exon alignments generated, we used those that included 85–100% of the samples for phylogenetic reconstructions (216 in total; Supporting Information Appendix S1, Methods S1.1). The 85% threshold was chosen to avoid having an excess of missing data in the analyses. Filtering out alignments did not exclude samples; therefore, all the 237 samples were present in the phylogenetic analyses. Alignment quality was verified visually before conducting downstream analyses.

A summary of the three methods we applied to reconstruct phylogenies is presented next, and more details are provided in the Supporting Information (Appendix S1, Methods S1.2). We generated: (1) a coalescence-based species tree (ASTRAL tree) from a set of gene trees using ASTRAL v.5.6.3 (Zhang et al., 2018); (2) a maximum likelihood (ML) tree using RAxML (Stamatakis, 2014) with the GTRGAMMA model, which we calibrated following the penalized likelihood approach by Paradis et al. (2004) with 12 calibration points (Supporting Information Appendix S1, Table S1.2) and a strict clock model (Supporting Information Appendix S1, Table S1.3); and (3) a Bayesian inference (BI) tree, where phylogenetic relationships and divergence times were estimated simultaneously using BEAST v.1.8.3 and the same calibration points used to generate the ML tree. Concatenated alignments were used in the ML and BI analyses. These three approaches yielded similar results, and the BI tree was used for downstream analyses.

2.3 | Biogeographical analyses

The ML-based dispersal-extinction-cladogenesis model (DEC; Ree & Smith, 2008) was applied to reconstruct the biogeographical history of Central American palms on the BI tree using the R package BioGeoBEARS (Matzke, 2014). Species distributions were obtained from the Global Biodiversity Information Facility (<http://>

doi.org/10.15468/dl.etlpb3), cleaned, and corroborated against distribution data from the literature (see details in Supporting Information Appendix S1, Methods S1.3). Biogeographical areas were delimited as: non-Neotropical areas, northern Central America, the Caribbean islands, southern Central America (including northern Chocó, given that this region emerged as part of the Panama Isthmus; Montes et al., 2015) and South America (see details in Supporting Information Appendix S1, Methods S1.3). Given that southern Central America had not emerged before 25 Ma (Montes et al., 2015), we time stratified the analysis before and after 25 Ma and applied dispersal-cost matrices, in which the probability of colonizing southern Central America before 25 Ma was set to zero, whereas the probability of all other dispersal events before and after 25 Ma was set to one.

We identified four radiations in Central America from the biogeographical analyses (clades I–IV; Figure 1). To visualize the timing of their diversification and address our first question, we plotted lineage-through-time (LTT) curves from each clade, starting from the node reconstructed as the first colonization event of Central America. We sampled 100 random trees from the pool of BI trees (burn-in excluded). For each of the 100 trees and for each of the clades, we excluded the taxa not belonging to a given clade with the `drop.tip()` function of the `ape` package (Paradis & Schliep, 2019). The same operation was performed on the BI tree. To plot all the LTTs of a given clade and the BI tree overlapping, we first plotted the LTT curve of the first sample with the `ape` function `ltt.plot()`. We then added the remaining 99 LTT lines and that of the BI tree with the `ape` function `ltt.lines()`.

2.4 | Phylogenetic diversity metrics

To address our second question, we investigated whether Central American palm species were phylogenetically clustered or scattered. Clustered taxa would indicate high local diversification, whereas scattered taxa would support high rates of dispersal, with the caveat that in both cases the effect of extinction cannot be excluded. Phylogenetic diversity metrics, which measure the level of species clustering in a phylogeny in relationship to their geographical distribution (Webb et al., 2002), were estimated for the BI tree using the same areas as defined for the biogeographical analyses. The following phylogenetic diversity metrics were estimated with the R package `picante` (Kembel et al., 2010): phylogenetic diversity *sensu stricto* (PD_{ss}) as the total phylogenetic branch length (measured in nucleotide substitutions) across species in a given region; the mean pairwise phylogenetic distance between species (MPD); the mean nearest taxon distance (MNTD); and their equivalents standardized for species richness (*ses.PD*, *ses.MPD* and *ses.MNTD*; Dexter et al., 2017; Honorio Coronado et al., 2015; Webb, 2000). The null model to which observed data were compared was “phylogeny.pool”, which randomizes the community data matrix by drawing from the pool of species occurring in the phylogeny. Observed values of the different metrics are negative when taxa are clustered in the tree in relationship to geography and positive when they are scattered. A *p*-value resulting from the comparison of observed versus expected

values determines the statistical significance of the results. A *p*-value < .05 was considered significant for clustered metric values, whereas a *p*-value > .95 was considered significant for scattered metric values.

2.5 | Timing of diversification in other Central American plant lineages

To place the results of the diversification of palms into the broader context of plant diversification, we used the World Checklist of Vascular Plants (WCVP, 2021, accessed 5 November 2020) to classify seed plant species as Central or South American [if present in any World Geographical Scheme for Recording Plant Distributions (WGSRPD) level three regions from Central and South America, respectively]. We classified species as present in Central America if they naturally occurred in any or multiple of the following areas: MXC, MXG, MXS, MXT, BLZ, COS, CPI, ELS, GUA, HON, NIC and PAN (Supporting Information Appendix S1, Figure S1.2). We considered species occurring inside Central America but with ranges extending outside the region as present in Central America. We then combined this information with a large-scale phylogeny of seed plants comprising 79,881 tips, based on molecular data from GenBank and a backbone from the Open Tree of Life (“GBOTB”; Smith & Brown, 2018), and used the `CladeByTrait` function of the `speciesgeocodeR` R package v.2.0-10 (Töpel et al., 2017) to extract clades with between 10 and 100 extant species (tips) and ≥85% of them in Central America. We then pruned species absent in Central America from these phylogenies and generated one LTT plot for each clade. We obtained the families of species from the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020) and used the `ape` (Paradis et al., 2004), `tidyverse` (Wickham et al., 2019) and `geiger` (Pennell et al., 2014) R packages for data handling and analysis.

3 | RESULTS

3.1 | Sampling, data processing and phylogenetic reconstruction

The phylogeny generated for this study represented 88% of the palm tribes, 69% of the genera and 29% of all the species described for the Americas. Importantly, our sampling included 54% of the palm species reported for Central America and 80% of the species reported for Panama. Species in our phylogeny constitute a representative sampling of the proportions of Central American endemics versus global species richness (Supporting Information Appendix S1, Figure S1.3).

We obtained 780,087 raw DNA reads (deposited in the Short Read Archive of the National Center for Biotechnology Information with the reference PRJNA535438). Statistics resulting from the different bioinformatic steps are presented in the Supporting Information (Appendix S1, Table S1.4). Locus recovery varied among samples by two orders of magnitude. An average of 11% (5.7–26.4%) of the reads per sample were discarded after cleaning steps. Taxonomic

bias in the hybridization of the probes (Heyduk et al., 2015) was observed in the subfamily Arecoideae, for which more loci were recovered than for other subfamilies (Supporting Information Appendix S1, Figure S1.4), probably attributable to the design of the probes being based mainly on the genome of the oil palm, which is a member of this subfamily. Within Arecoideae, targets were sequenced homogeneously (Supporting Information Appendix S1, Figure S1.4, lineages Bactridinae, Chamaedoreae and Geonomateae).

Our ASTRAL, ML and BI trees yielded congruent topologies (Supporting Information Appendix S1, Figures S1.5– S1.9; NEXUS formatted trees available at: [10.5281/zenodo.5767228](https://doi.org/10.5281/zenodo.5767228)). Minor differences among inference methods, mainly at the species level, were poorly supported in general (LPPs <.9; bootstrap values <90%; posterior probabilities <.9). The relationships between subfamilies, tribes and genera were consistent among trees, as were clades within genera. In particular, clades I–IV (Figure 1) were recovered with strong support for all three methods. Both ML and BI dated trees showed congruent divergence times (Supporting Information Appendix S1, Figure S1.10).

3.2 | Age of Central American palm lineages

Our BI tree resulted in a median node age for the crown of the palm family at 131 Ma [95% highest posterior density (HPD) = 137–126 Ma], the stem of Bactridinae at 45.9 Ma (95% HPD = 47.4–44.1 Ma), the crown of Bactridinae at 32.4 Ma (95% HPD = 33.3–31.7 Ma), the stem of Chamaedoreae at 81.8 Ma (95% HPD = 84.3–79.2 Ma), the crown of Chamaedoreae at 42.3 Ma (95% HPD = 44.9–39.9 Ma), the stem of Geonomateae at 49.7 Ma (95% HPD = 52.4–46.8 Ma) and the crown of Geonomateae at 28.6 Ma (95% HPD = 30.3–26.7 Ma). Our geographical range evolution analyses placed the most recent common ancestor (MRCA) of American arecoids in South America in the Cretaceous, from where lineages dispersed to Central America (north and south), the Caribbean islands and other regions (Figure 1; Supporting Information Appendix S1, Figure S1.11). Furthermore, our results implied that the first colonization of Central America occurred in the Eocene (42.3 Ma), when the MRCA of tribe Chamaedoreae dispersed to Central America and other regions. Within this tribe, four dispersal events from the north to the south of Central America were

inferred for the last 10 Ma. During the Miocene, 11 Bactridinae and 12 Geonomateae dispersal events from South America to Central America (mainly to the south) were inferred. Species diversification in Central America started in the Miocene (Figure 1) with the radiation of *Chamaedorea* (c. 12 Ma; clade I), followed by the synchronized diversification of *Calyptrogyne* (clade II) and the Central American *Bactris* (clade IV) and *Geonoma* (clade III) c. 8–7 Ma.

3.3 | Phylogenetic diversity metrics

Our results identified that Central American species are significantly clustered in the phylogeny (Table 2; Supporting Information Appendix S1, Tables S1.5 and S1.6). Stronger phylogenetic clustering occurs in the southern part of Central America according to the metrics sesPD (Table 2) and sesMPD (Supporting Information Appendix S1, Table S1.5). The sesMNTD metric (Supporting Information Appendix S1, Table S1.6) showed higher clustering in northern Central America.

3.4 | Timing of diversification of other plant families in Central America

From the seed plant phylogeny by Smith and Brown (2018), we identified 54 Central American clades with 979 Central American species, belonging to 90 genera and 26 plant families. The average number of extant Central American species was 18.1 per clade, and the average age was 6.48 Myr (Figure 2). All clades were younger than 15 Myr, except for two lineages: (1) *Anthurium* (Araceae), 17.5 Myr; and (2) a clade comprising the Annonaceae genera *Desmopsis*, *Stenanona*, *Tridimeris* and *Sapranthus*, 29.58 Myr.

4 | DISCUSSION

4.1 | A reliable, robust and precise evolutionary framework for Central American palms

Our results indicate that genomic data are crucial to resolving the evolutionary history of palms at all taxonomic levels, particularly regarding species relationships (Supporting Information Appendix

TABLE 2 Standardized effect size phylogenetic diversity (sesPD) estimated from the Bayesian inference phylogeny of Central American palms (Arecaceae) reconstructed for this study

Area	Number of taxa	PD observed	PD observed z	PD observed p-value
Central America (north)	60	1,166.7625	-1.743061	.053*
Central America (south)	118	1,787.7156	-2.625103	.01**
South America	114	2,076.0288	0.2607252	.594
West Indies	20	956.4148	2.3254116	.993††
Other	9	653.8557	2.7323751	.993††

Note. Asterisks indicate whether the p-value is statistically significant for clustered species in the phylogeny (negative values of PD observed z, and * $p < .1$, ** $p < .05$) or scattered species in the phylogeny (positive values of PD observed z, and † $p > .90$, †† $p > .95$).

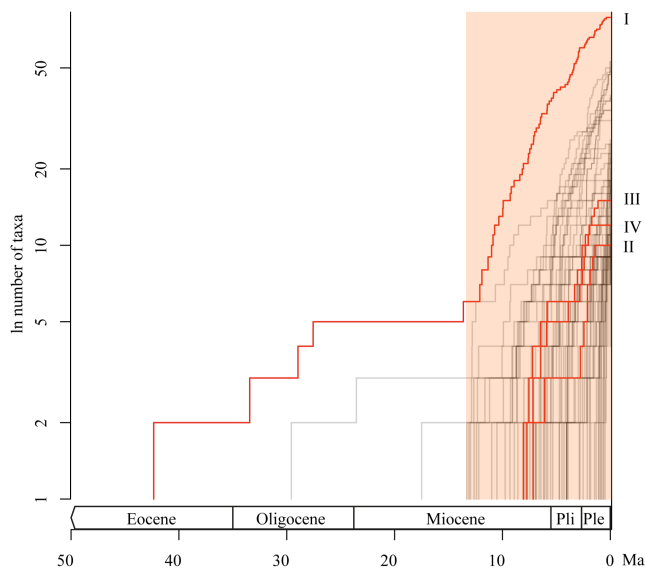


FIGURE 2 Lineage-through-time (LTT) plots of 54 predominantly Central American clades. Each black line represents a clade extracted from a mega-phylogeny of seed plants (Smith & Brown, 2018); the red lines show the LTT plots of palm clades I–IV (Figure 1) extracted from the Bayesian inference phylogeny reconstructed for this study. The orange box indicates the main period of species diversification starting at c. 13 Ma, during which 99.0% of all speciation events took place (99.5% in the seed plants phylogeny and 95.5% in palm clades)

S1, Discussion S1.1). The large amount of data generated for this study in terms of sampling (237 samples, 218 species) and number of base pairs (c. 130 DNA kb/sample) represent a massive increase in the quantity of data for phylogenetic reconstruction in palms. This phylogenetic framework is reliable, because relationships among subfamilies and tribes agree with previous reconstructions based on markers that are not in our dataset (e.g., Baker et al., 2009), meaning that palm classification is reaching stability. Our tree is also the most coherent reconstruction of American palm evolution, because this is the first time that such a broad sampling, large quantity of data and high number of calibration points have been combined in one analysis.

Our tree is more robust relative to those estimated by Antonelli et al. (2017), Baker and Couvreur (2013) and Faurby et al. (2016) in terms of node support at deep (Supporting Information Appendix S1, Figure S1.12) and shallow (Figure 3) phylogenetic relationships. Node support among species is strong overall (bootstrap > 85%, posterior probabilities > .95), and support within genera is higher than in previous species-level phylogenies of palms estimated from Sanger sequencing data (Figure 3; Faurby et al., 2016; Antonelli et al., 2017). Our use of 12 time-calibration points and a comparison of two dating methods permitted a divergence time estimation that is considerably more precise than previous estimates (i.e. with shorter 95% HPD node heights; Supporting Information Appendix S1, Figures S1.13 and S1.14; Antonelli et al., 2017; Baker & Couvreur, 2013; Faurby et al., 2016). By using more calibration points than in previous studies, our divergence time estimation is also likely to be

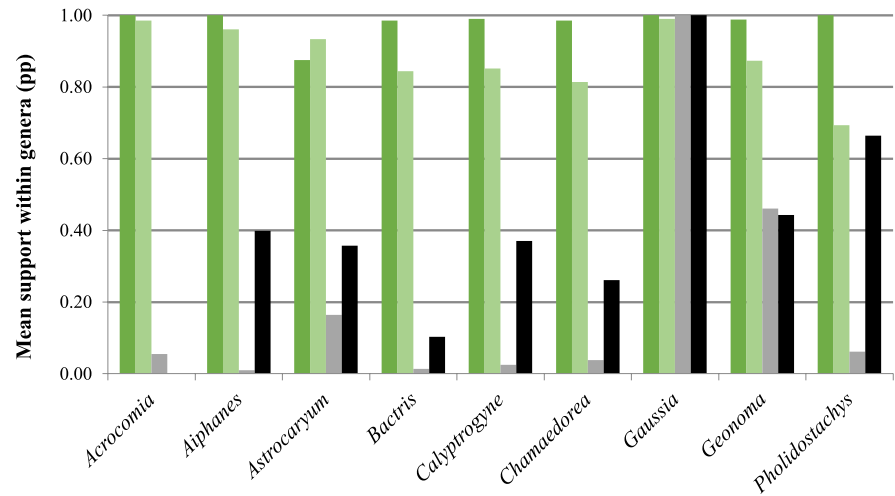
more accurate, although using more fossils could be a source of error if they are not correctly placed or identified (Magallón, 2014; Schönenberger et al., 2020; Yang & Rannala, 2006). To reduce this potential effect, we chose our calibration points following previous studies (Supporting Information Appendix S1, Table S1.2), applying informative priors when their placement had been thoroughly evaluated (e.g., Baker & Couvreur, 2013; Cano et al., 2018; Couvreur et al., 2011). Less informative priors were applied to fossils used at a smaller taxonomic scale or in less detailed studies (e.g., Antonelli et al., 2017; Eiserhardt et al., 2011; Roncal et al., 2013), to reduce their effect on the overall analysis while still informing the Bayesian reconstruction (Nascimento et al., 2017).

For a detailed discussion on palm systematics, see the Supporting Information (Appendix S1, Discussion S1.1; Table S1.7; Figures S1.15 and S.16). The ML and BI trees yielded similar topological results regarding the subfamily and tribe levels (Supporting Information Appendix S1, Figure S1.15), although some differences were detected within tribe Cocoseae. Overall, the phylogenetic relationships observed at a deep taxonomic level coincide with previous palm phylogenies (Baker et al., 2009; Comer et al., 2015, 2016). All the palm genera included in our analyses with more than one sample per genus were reconstructed as monophyletic, except for *Calyptrotrichia*, which would be paraphyletic as previously reported (Loiseau et al., 2019; Roncal et al., 2012). The intergeneric relationships reconstructed in our analyses were strongly supported in most of the cases (Supporting Information Appendix S1, Figure S1.15). An exception is the genera within Bactridinae, whose relationships are contentious, showing different topologies between ML and BI and low support in ML. The topologies presented by other phylogenies including these genera (e.g. Baker et al., 2009; Eiserhardt et al., 2011) do not coincide with the ones presented here. Although our BI analysis shows strong support for the reconstructed topology, a closer inspection of molecular data, accounting for the possibility of incongruences between gene histories, would be recommended to resolve these branches confidently. Relationships among the genera in Chamaedoreae coincide with the topology presented by Cuenca et al. (2008). Within Geonomateae, the same generic relationships were reconstructed by Roncal et al. (2012) from three nuclear regions. Loiseau et al. (2019) reconstructed a different topology from genomic data. What is consistent among the three reconstructions is that *Pholidostachys* is sister to all other Geonomateae and *Welfia* is sister to all Geonomateae excluding *Pholidostachys*. The species-level phylogenetic relationships presented here are, in many cases, novel because our sampling includes several taxa that have never been sequenced before. However, there are some topological similarities with previous studies of Bactridinae, Chamaedoreae and Geonomateae (Supporting Information Appendix S1, Discussion S1.1, Table S1.7).

4.2 | Extant understorey palm diversity of Central America is young

Our results identify that although some palm lineages had already dispersed into Central America by the Eocene, diversification of

FIGURE 3 Comparison of node support values obtained between this and two other studies with less inclusive genetic sampling. Plots show posterior probabilities (pp) for our analyses based on genomic data (green; Bayesian inference tree) and previous estimates by Faurby et al. (2016; grey) and Antonelli et al. (2017; black) based on commonly used molecular markers



the extant palm lineages began only in the Miocene (Figure 1; Supporting Information Appendix S1, Figure S1.11). Our ancestral range estimation indicates that Chamaedoreae colonized northern Central America during the Eocene at c. 42 Ma. An early presence of palms in Central America since the Eocene is supported by a single palm fossil (Herrera et al., 2012) that cannot be assigned to a particular extant lineage within palms nor to a specific habitat (e.g., rain forest or coastal environments). It is therefore not clear whether this was an understory species. Our reconstruction suggests that Chamaedoreae persisted in northern Central America, apparently without substantial diversification until 12 Ma, when diversification increased, particularly in *Chamaedorea* (see more on this below). In striking synchrony, three other diversification bursts in Central America occurred in *Bactris*, *Calyptrogyne* and *Geonoma* (Figure 1, bottom) between 7 and 8 Ma. The fossil record also attests to a high Miocene palm diversity (22 taxa; Jaramillo et al., 2014). Taken together, our results and the scarce Palaeogene palm fossil record (one taxon) led to rejection of our null hypothesis that Central American understory palms mostly diversified during the Eocene (Table 1). Instead, our results show an increase of species richness during the Miocene, and the fossil record shows a high Miocene palm diversity, suggesting that diversification of the palm flora occurred more recently.

The time lag of c. 30 Myr between the first colonization event of Chamaedoreae into northern Central America and the onset of their diversification (note the few branching events and long branches) is therefore in need of explanation. However, what the phylogenetic relationships of extant species fail to show is the potential impact of extinction on the patterns observed. Indeed, long branches in phylogenies could indicate high, steady extinction rates or even the effect of mass extinction events (Antonelli & Sanmartín, 2011; Crisp & Cook, 2009). The long branches in Chamaedoreae could therefore be the signature of diversity loss from the Eocene until the late Miocene. A wave of extinctions might have been triggered by the sudden decline in temperature at the end of the Eocene (35 Ma). This event affected the boreotropical flora of the early Eocene (Morley, 2003) and has been suggested as the cause of mass

extinction in coryphoid palms distributed in Central America and the Caribbean (Cano et al., 2018). Further palaeontological evidence from the region, in particular time series of vegetation changes (including diversity and abundance), would be necessary to test this hypothesis.

Recent, late-Miocene radiations in South America have been detected in phylogenies of other taxa (e.g., Kay et al., 2005; Koenen et al., 2015; Richardson et al., 2001), although it is known from the local fossil record that Eocene Amazonian TRFs were even more diverse than extant TRFs (Jaramillo et al., 2006, 2010; Wilf et al., 2003). Hence, the high diversity of South American TRFs might not be a recent phenomenon, but might have been maintained through high species turnover (Koenen et al., 2015). Although the Eocene palm fossil record available from northern Central America does not show such diversity levels, high species turnover and an associated high extinction rate cannot be excluded as a cause of the time lag in the diversification of Chamaedoreae.

Our results demonstrate that palms are adequate indicators of diversification processes in Central America, because our findings with palms are corroborated by our cross-taxonomic analysis showing that 54 seed plant lineages, predominantly distributed in Central America, also underwent major diversification in the second half of the Miocene (Figure 2), with 99.5% of all speciation events being <13 Ma. We acknowledge that these cross-taxonomic results based on a comprehensive dated phylogeny of seed plants (Smith & Brown, 2018) might be influenced by taxonomic uncertainty and that the necessary focus on primarily Central American clades (85% of all tips; see Materials and methods section) might bias the dataset towards younger clades. Yet, a strong diversification of plants in Central America during the Miocene is also reflected by the rich Miocene fossil record of central Panama (Jaramillo et al., 2014). There is a striking temporal coincidence between this phase of diversification and the proposed progressive closure of the Central American Seaway that separated South and Central America until c. 15–10 Ma, as revealed from rich geological (Montes et al., 2015) and palaeontological (Jaramillo, 2018) data. Land emergence connecting those previously separated landmasses was likely to trigger

the Great American Biotic Interchange (Bacon et al., 2015), and our study suggests that this was also a major trigger for diversification in Central American TRFs, where lineages arriving from the south diversified extensively.

4.3 | The majority of Central American palm diversity evolved locally

Our geographical range reconstruction confirms that dispersal contributed to the current palm diversity in Central America, which can be attributed to the position of the region as a land bridge between two continents. Our analysis detected 35 independent dispersal events to the area, all of them from South America. Palms followed two colonization routes into Central America: (1) a dispersal event from South America to northern Central America was followed by a southward colonization of Central America coinciding with the gradual emergence of terrestrial habitats in the same direction (Gutiérrez-García & Vázquez-Domínguez, 2013; Montes et al., 2015); and (2) repeated, independent northward colonization from South to Central America occurred concomitantly with the formation of the Isthmus of Panama during the Miocene (Montes et al., 2015). The importance of South America as a source of lineages in Central America was proposed by Gentry more than three decades ago based on the floristic composition of the area (Gentry, 1985). Further support for this scenario comes from biogeographical analyses showing that numerous species in Central America, particularly in the south, originated in Amazonia (Antonelli et al., 2018) and the Andes (Pérez-Escobar et al., 2019).

It is clear from our results that dispersal was a fundamental process in the assembly of palm diversity in Central America, especially during its early history. However, these results also show that local diversification is responsible for most of the extant species richness, because the dispersal versus local diversification events ratio was estimated as 1:3 for the entire phylogeny (35 colonization events into Central America vs. 103 local diversification events) and as 1:4 if only events happening within our target clades are considered (26 colonization events into Central America vs. 101 local diversification events). The preponderant role of local diversification is clearly visible in our phylogeny, with Central American species strongly clustered (Figure 1). Further support comes from the different phylogenetic diversity metrics estimated, which show that the geographical clustering is significant in relationship to Central America (Table 2; Supporting Information Appendix S1, Tables S1.5 and S1.6).

These phylogenetic diversity metrics depend on the provenance of the sampling included in the phylogeny, which does not comprise all the species in our three targeted clades. However, given that our sampling is proportional to the Central American endemic versus the global number of species (Supporting Information Appendix S1, Figure S1.3), our phylogenetic diversity clustering results arguably provide a fair representation of natural patterns. Furthermore, the addition of missing species might

alter the results depending on: (1) whether the species are Central American endemics or not; and (2) on their phylogenetic placement as clustered or not to Central American species. Regarding point 1, among the missing species from our targeted clades, 92% are endemic to Central America. Regarding point 2, only a few of them have previously been included in molecular phylogenies (Supporting Information Appendix S1, Discussion S1.1), where they are generally placed as closely related to species belonging to one of our four identified radiations (Figure 1, clades I–IV). Therefore, the addition of missing species would probably enhance the patterns revealed by the phylogenetic diversity metrics.

These results suggest that although there is some support for our alternative hypothesis, given the multiple initial dispersal events to Central America, our null hypothesis (that a small number of dispersal events from neighbouring areas was followed by intense local diversification; Table 1) cannot be rejected. Such a phylogenetic clustering in Central America was also detected in a global, genus-level phylogeny of palms (Kissling et al., 2012) and in other TRF plant groups, such as *Inga*, *Swartzia* (both in Fabaceae) and *Protieae* (Burseraceae; Dexter et al., 2017). Local diversification of these clades might have been favoured by biome turnover between TRF and savanna occurring from the late Miocene all the way to the Pleistocene (Bacon et al., 2015, 2016; Smith & Klicka, 2010), which could have spurred speciation through repeated vicariance and dispersal events related to habitat shifts between biomes.

4.4 | Conclusions

Our results, based on unprecedented taxonomic and genetic sampling in palms, indicate that most palm species that characterize the hyperdiverse TRFs of Central America today evolved locally after repeated colonization events to the area, mostly from South America following the emergence of land across the Isthmus of Panama. Evidence revealed by our analyses and the palm fossil record, alongside 54 other seed plant lineages, suggests that TRFs in Central America became hyperdiverse only from 12–6 Ma, in contrast to South American TRFs, which have been diverse since the Palaeocene (58 Ma).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

The study was conceived by Á.C., M.P., A.A., F.W.S. and C.D.B. The data were collected by Á.C., I.M.L. and H.L. and analysed by Á.C., T.A., A.Z., C.C. and M.T. The manuscript was written by Á.C., A.A. and M.P. and reviewed by C.D.B., I.M.L., T.A. and F.W.S.

DATA AVAILABILITY STATEMENT

Short Read Archive (SRA) of the National Center for Biotechnology Information, reference PRJNA535438. Scripts and input data are available at 10.5281/zenodo.5767228.

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REFERENCES

- Andermann, T., Cano, Á., Zizka, A., Bacon, C., & Antonelli, A. (2018). SECAPR—A bioinformatics pipeline for the rapid and user-friendly processing of targeted enriched Illumina sequences, from raw reads to alignments. *PeerJ*, 6, e5175.
- Andrews, S. (2010). *FastQC: A quality control tool for high throughput sequence data* [Online]. <http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>
- Antonelli, A., Hettling, H., Condamine, F. L., Vos, K., Nilsson, R. H., Sanderson, M. J., Sauquet, H., Scharn, R., Silvestro, D., Töpel, M., Bacon, C. D., Oxelman, B., & Vos, R. A. (2017). Toward a self-updating platform for estimating rates of speciation and migration, ages, and relationships of taxa. *Systematic Biology*, 66, 152–166.
- Antonelli, A., & Sanmartín, I. (2011). Mass extinction, gradual cooling, or rapid radiation? Reconstructing the spatiotemporal evolution of the ancient *Angiosperm genus Hedyosmum* (Chloranthaceae) using empirical and simulated approaches. *Systematic Biology*, 60, 596–615.
- Antonelli, A., Zizka, A., Carvalho, F. A., Scharn, R., Bacon, C. D., Silvestro, D., & Condamine, F. L. (2018). Amazonia is the primary source of neotropical biodiversity. *Proceedings of the National Academy of Sciences*, 115, 6034–6039.
- Bacon, C. D., Molnar, P., Antonelli, A., Crawford, A. J., Montes, C., & Vallejo-Pareja, M. C. (2016). Quaternary glaciation and the great American biotic interchange. *Geology*, 44, 375–378.
- Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., & Antonelli, A. (2015). Biological evidence supports an early and complex emergence of the isthmus of Panama. *Proceedings of the National Academy of Sciences*, 112, 6110–6115.
- Baker, W. J., & Couvreur, T. L. P. (2013). Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography*, 40, 274–285.
- Baker, W. J., Savolainen, V., Asmussen-Lange, C. B., Chase, M. W., Dransfield, J. B., Forest, F., Harley, M. M., Uhl, N. W., & Wilkinson, M. (2009). Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology*, 58, 240–256.
- Barthlott, W., Hostert, A., Kier, G., Küper, W., Kreft, H., Mutke, J., Rafiqpoor, M. D., & Sommer, J. H. (2007). Geographic patterns of vascular plant diversity at continental to global scale. *Erdkunde*, 61, 305–315.
- Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics (Oxford, England)*, 30, 2114–2120.
- Cano, Á., Bacon, C. D., Stauffer, F. W., Antonelli, A., Serrano-Serrano, M. L., & Perret, M. (2018). The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. *Journal of Biogeography*, 45, 1432–1443.
- Comer, J. R., Zomlefer, W. B., Barrett, C. F., Davis, J. I., Stevenson, D. W., Heyduk, K., & Leebens-Mack, J. H. (2015). Resolving relationships within the palm subfamily Arecoideae (Arecaceae) using plastid sequences derived from next-generation sequencing. *American Journal of Botany*, 102, 888–899.
- Comer, J. R., Zomlefer, W. B., Barrett, C. F., Stevenson, D. W., Heyduk, K., & Leebens-Mack, J. H. (2016). Nuclear phylogenomics of the palm subfamily Arecoideae (Arecaceae). *Molecular Phylogenetics and Evolution*, 97, 32–42.
- Condit, R., Perez, R., Aguilar, S., Lao, S., Foster, R., & Hubbell, S. (2019). *Complete data from the Barro Colorado 50-ha plot: 423617 trees, 35 years*. Dryad Dataset, <https://doi.org/10.15146/5xcp-0d46>
- Couvreur, T. L. P., Forest, F., & Baker, W. J. (2011). Origin and global diversification patterns of tropical rain forests: Inferences from a complete genus-level phylogeny of palms. *BMC Biology*, 9, 44.
- Crisp, M. D., & Cook, L. G. (2009). Explosive radiation or cryptic mass extinction? Interpreting signatures in molecular phylogenies. *Evolution*, 63, 2257–2265.
- Cuenca, A., Asmussen-Lange, C. B., & Borchsenius, F. (2008). A dated phylogeny of the palm tribe Chamaedoreae supports Eocene dispersal between Africa, north and South America. *Molecular Phylogenetics and Evolution*, 46, 760–775.
- de Sousa, F., Bertrand, Y. J. K., Nylinder, S., Oxelman, B., Eriksson, J. S., & Pfeil, B. E. (2014). Phylogenetic properties of 50 nuclear loci in *Medicago* (Leguminosae) generated using multiplexed sequence capture and next-generation sequencing. *PLoS One*, 9, e109704.
- Dexter, K. G., Lavin, M., Torke, B. M., Twyford, A. D., Kursar, T. A., Coley, P. D., Drake, C., Hollands, R., & Pennington, R. T. (2017). Dispersal assembly of rain forest tree communities across the Amazon basin. *Proceedings of the National Academy of Sciences*, 114, 2645–2650.
- Eiserhardt, W. L., Pintaud, J.-C., Asmussen-Lange, C. B., Hahn, W. J., Bernal, R., Balslev, H., & Borchsenius, F. (2011). Phylogeny and divergence times of Bactridinae (Arecaceae, Palmae) based on plastid and nuclear DNA sequences. *Taxon*, 60, 485–498.
- Erkens, R. H. J., Chatrou, L. W., & Couvreur, T. (2012). Radiations and key innovations in an early branching angiosperm lineage (Annonaceae; Magnoliales). *Botanical Journal of the Linnean Society*, 169, 117–134.
- Faurby, S., Eiserhardt, W. L., Baker, W. J., & Svenning, J.-C. (2016). An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution*, 100, 57–69.
- Freiberg, M., Winter, M., Gentile, A., Zizka, A., Muellner-Riehl, A. N., Weigelt, A., & Wirth, C. (2020). LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. *Scientific Data*, 7, 416. <https://doi.org/10.1038/s41597-020-00702-z>
- Gentry, A. H. (1982). Neotropical floristic diversity: Phytogeographical connections between central and South America, pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, 69, 557–593.
- Gentry, A. H. (1985). In W. G. D'Arcy & M. Correa (Eds.), *Contrasting phylogenetic patterns of upland and lowland Panamanian plants. The botany and natural history of Panama* (pp. 147–160). Missouri Botanical Garden Press.
- Gomez-Navarro, C., Jaramillo, C., Herrera, F., Wing, S. L., & Callejas, R. (2009). Palms (Arecaceae) from a Paleocene rainforest of northern Colombia. *American Journal of Botany*, 96, 1300–1312.

- Govaerts, R., Dransfield, J., Zona, S., Hodel, D. R., & Henderson, A. (2021). *World checklist of Areaceae*. Facilitated by the Royal Botanic Gardens Published on the Internet. *World Checklist of Areaceae*.
- Gutiérrez-García, T. A., & Vázquez-Domínguez, E. (2013). Consensus between genes and stones in the biogeographic and evolutionary history of Central America. *Quaternary Research*, *79*, 311–324.
- Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences*, *115*, 7985–7990.
- Henderson, A. (2000). *Bactris* (Palmae). *Flora Neotropica*, *79*, 1–181.
- Henderson, A. (2011). A revision of *Geonoma* (Arecaceae). *Phytotaxa*, *17*, 1–271.
- Henderson, A., Galeano, G., & Bernal, R. (1995). *Field guide to the palms of the Americas*. Princeton University Press.
- Herrera, F., Manchester, S. R., & Jaramillo, C. (2012). Permineralized fruits from the late Eocene of Panama give clues of the composition of forests established early in the uplift of Central America. *Review of Palaeobotany and Palynology*, *175*, 10–24.
- Heyduk, K., Trapnell, D. W., Barrett, C. F., & Leebens-Mack, J. (2015). Phylogenomic analyses of species relationships in the genus *Sabal* (Arecaceae) using targeted sequence capture. *Biological Journal of the Linnean Society*, *117*, 106–120.
- Hodel, D. R. (1992). *Chamaedorea palms, the species and their cultivation*. Allen Press.
- Honorio Coronado, E. N., Dexter, K. G., Pennington, R. T., Chave, J., Lewis, S. L., Alexiades, M. N., Alvarez, E., Alves de Oliveira, A., Amaral, I. L., Araujo-Murakami, A., Arets, E. J. M. M., Aymard, G. A., Baraloto, C., Bonal, D., Brienen, R., Cerón, C., Cornejo Valverde, F., Di Fiore, A., Farfan-Rios, W., ... Phillips, O. L. (2015). Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions*, *21*, 1295–1307.
- Jaramillo, C., Moreno, E., Ramírez, V., da Silva, S., Barrera, A., Barrera, A., Moron, S., Herrera, F., Escobar, J., Koll, R., Manchester, S. R., & Hoyos, N. (2014). Palynological record of the last 20 million years in Panama. In W. D. Stevens, O. M. Montiel, & P. Raven (Eds.), *Paleobotany and biogeography: A festschrift for Alan Graham in his 80th year* (pp. 134–251). Missouri Botanical Garden Press.
- Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., Parra, F. de la, Morón, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvarán, M., Osorno, J., Crowley, J.L., Valencia, V. & Vervoort, J. (2010) Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science*, *330*, 957–961.
- Jaramillo, C., Rueda, M. J., & Mora, G. (2006). Cenozoic plant diversity in the neotropics. *Science*, *311*, 1893–1896.
- Jaramillo, C. A. (2018). Evolution of the isthmus of Panama: Biological, palaeoceanographic and palaeoclimatological implications. In C. Hoorn, A. Perrigo, & A. Antonelli (Eds.), *Mountains, climate and biodiversity* (pp. 323–338). John Wiley & Sons.
- Kay, K. M., Reeves, P. A., Olmstead, R. G., & Schemske, D. W. (2005). Rapid speciation and the evolution of hummingbird pollination in neotropical *Costus subgenus Costus* (Costaceae): Evidence from nrDNA ITS and ETS sequences. *American Journal of Botany*, *92*, 1899–1910.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.
- Kissling, W. D., Eiserhardt, W. L., Baker, W. J., Borchsenius, F., Couvreur, T. L. P., Balslev, H., & Svenning, J.-C. (2012). Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences*, *109*, 7379–7384.
- Koenen, E. J. M., Clarkson, J. J., Pennington, T. D., & Chatrou, L. W. (2015). Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. *New Phytologist*, *207*, 327–339.
- Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics*, *25*, 1754–1760.
- Loiseau, O., Olivares, I., Paris, M., de La Harpe, M., Weigand, A., Koubínová, D., Rolland, J., Bacon, C. D., Balslev, H., Borchsenius, F., Cano, A., Couvreur, T. L. P., Delnatte, C., Fardin, F., Gayot, M., Mejía, F., Mota-Machado, T., Perret, M., Roncal, J., ... Salamin, N. (2019). Targeted capture of hundreds of nuclear genes unravels phylogenetic relationships of the diverse neotropical palm tribe geonomateae. *Frontiers in Plant Science*, *10*. <https://doi.org/10.3389/fpls.2019.00864>
- Magallón, S. (2014). A review of the effect of relaxed clock method, long branches, genes, and calibrations in the estimation of angiosperm age. *Botanical Sciences*, *92*, 1–22.
- Matthews, K. J., Maloney, K. T., Zahirovic, S., Williams, S. E., Seton, M., & Müller, R. D. (2016). Global plate boundary evolution and kinematics since the late Paleozoic. *Global and Planetary Change*, *146*, 226–250.
- Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island clades. *Systematic Biology*, *63*, 951–970.
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., Ayala, C., Pérez-Angel, L. C., Rodriguez-Parra, L. A., Ramirez, V., & Niño, H. (2015). Middle Miocene closure of the central American seaway. *Science*, *348*, 226–229.
- Moonlight, P. W., Richardson, J. E., Tebbitt, M. C., Thomas, D. C., Hollands, R., Peng, C.-I., & Hughes, M. (2015). Continental-scale diversification patterns in a megadiverse genus: The biogeography of neotropical *begonia*. *Journal of Biogeography*, *42*, 1137–1149.
- Morley, R. J. (2003). Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*, 5–20.
- Nascimento, F. F., Reis, M. d., & Yang, Z. (2017). A biologist's guide to Bayesian phylogenetic analysis. *Nature Ecology & Evolution*, *1*, 1446–1454.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics (Oxford, England)*, *20*, 289–290.
- Paradis, E., & Schliep, K. P. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.
- Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., Alfaro, M. E., & Harmon, L. J. (2014). Geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, *30*, 2216–2218.
- Pérez-Escobar, O. A., Lucas, E., Jaramillo, C., Monro, A., Morris, S. K., Bogarín, D., Greer, D., Dodsworth, S., Aguilar-Cano, J., Sanchez Meseguer, A., & Antonelli, A. (2019). The origin and diversification of the hyperdiverse flora in the chocó biogeographic region. *Frontiers in Plant Science*, *10*, 1328.
- Perret, M., Chautems, A., De Araujo, A. O., & Salamin, N. (2013). Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. *Botanical Journal of the Linnean Society*, *171*, 61–79.
- Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*, 4–14.
- Richardson, J. E., Pennington, R. T., Pennington, T. D., & Hollingsworth, P. M. (2001). Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science (New York, N.Y.)*, *293*, 2242–2245.
- Roncal, J., Henderson, A., Borchsenius, F., Cardoso, S. R. S., & Balslev, H. (2012). Can phylogenetic signal, character displacement, or random phenotypic drift explain the morphological variation in the genus *Geonoma* (Arecaceae)? *Biological Journal of the Linnean Society*, *106*, 528–539.
- Roncal, J., Kahn, F., Millan, B., Couvreur, T. L., & Pintaud, J.-C. (2013). Cenozoic colonization and diversification patterns of tropical

- American palms: Evidence from *Astrocaryum* (Arecaceae). *Botanical Journal of the Linnean Society*, 171, 120–139.
- Schönenberger, J., von Balthazar, M., Martínez, A. L., Albert, B., Prieu, C., Magallón, S., & Sauquet, H. (2020). Phylogenetic analysis of fossil flowers using an angiosperm-wide data set: Proof-of-concept and challenges ahead. *American Journal of Botany*, 107, 1433–1448.
- Simpson, J. T., Wong, K., Jackman, S. D., Schein, J. E., Jones, S. J. M., & Birol, I. (2009). ABySS: A parallel assembler for short read sequence data. *Genome Research*, 19, 1117–1123.
- Smith, B. T., & Klicka, J. (2010). The profound influence of the late Pliocene Panamanian uplift on the exchange, diversification, and distribution of New World birds. *Ecography*, 33, 333–342.
- Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105, 302–314.
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
- ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomao, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J.-F., Monteagudo, A., Nunez Vargas, P., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., ... Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092.
- Töpel, M., Zizka, A., Calió, M. F., Scharn, R., Silvestro, D., & Antonelli, A. (2017). SpeciesGeoCoder: Fast categorization of species occurrences for analyses of biodiversity, biogeography, ecology, and evolution. *Systematic Biology*, 66, 145–151.
- WCVP. (2021). *World checklist of vascular plants, version 2.0*. Facilitated by the Royal Botanic Gardens, Kew.
- Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, 156, 145–155.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1686.
- Wilf, P., Cúneo, N. R., Johnson, K. R., Hicks, J. F., Wing, S. L., & Orladovich, J. D. (2003). High plant diversity in Eocene South America: Evidence from Patagonia. *Science*, 300, 122–125.
- Willis, C. G., Franzone, B. F., Xi, Z., & Davis, C. C. (2014). The establishment of central American migratory corridors and the biogeographic origins of seasonally dry tropical forests in Mexico. *Frontiers in Genetics*, 5, 433.
- Yang, Z., & Rannala, B. (2006). Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution*, 23, 212–226.
- Zhang, C., Rabiee, M., Sayyari, E., & Mirarab, S. (2018). ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19, 153.

BIOSKETCH

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SUPPORTING INFORMATION

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