



Editor's Choice Article

Phylogeny, historical biogeography and diversification rates in an economically important group of Neotropical palms: Tribe Euterpeae

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ABSTRACT

Tribe Euterpeae is an economically and ecologically important group of Neotropical palms (Arecaceae). Some species are hyperdominant in the Neotropics, and many constitute a good source of revenue. To reconstruct the biogeographical history and diversification of the Euterpeae, we inferred a robust dated molecular phylogenetic hypothesis including 82% of the species sequenced for five DNA regions (*trnD-trnT*, CISP4, WRKY6, RPB2, and PHYB). Ancestral range was estimated using all models available in BioGeoBEARS and Binary State Speciation and Extinction analysis was used to evaluate the association of biome and inflorescence type with diversification rates. All intergeneric relationships were resolved providing insight on the taxonomic controversy of *Jessenia*, *Euterpe* and *Prestoea*. Three widely distributed Neotropical species were non-monophyletic, inviting a revision of species circumscriptions. The Euterpeae started its diversification in the mid Eocene (40 Mya), with most species-level divergence events occurring in the last 10 million years. Four colonization events from Central to South America were inferred. Different diversification rates were associated with biomes. Lowland rainforest was inferred as the ancestral biome of Euterpeae, attesting to the importance of lowland adapted lineages on the assembly of the montane flora. The two-fold higher speciation rate for montane taxa (compared with lowland rainforest taxa) was contemporaneous to the Andean orogenic uplift. The specialized beetle pollination of *Oenocarpus* with its hippuriform (horsetail shape) inflorescence was not associated with diversification rates in Euterpeae.

1. Introduction

The Neotropics or tropical American region stretches across the North American, the Caribbean and South American plates, and harbors more birds, mammals and amphibians than tropical Africa and Asia (Jenkins et al., 2013). Phylogenetic-based biogeographic studies in the Neotropics have revealed numerous examples of biotic migrations and evolutionary connections among its composing biogeographic regions and biomes (e.g., Simon et al., 2009; Nieto-Blázquez et al., 2017; Schultz et al., 2017). Notably, Amazonia has been shown to represent a source area of emigrant lineages to other Neotropical regions, with lineages shifting across major biome types more often than previously thought (Crisp et al., 2009; Antonelli et al., 2018). The direction of transitions from forested/wet to open/dry Neotropical biomes is more

prevalent than the opposite direction (Simon et al., 2009; Antonelli et al., 2018).

Biome shifts have often been associated with changes in diversification rates (e.g., Koenen et al., 2013), but not always (e.g., Veranso-Libalah et al. 2018). The question of what prompts certain biome shifts to alter diversification rates can be better addressed by analyzing the evolution of the suite of traits that facilitate ecological shifts. These traits may be ecological pre-adaptations of migrating taxa (Wiens et al., 2010), or new physiological adaptations under new environments (Simon et al., 2009). In the Neotropics, two of the most important biomes are the montane and the lowland rainforest (sensu Olson et al., 2001). A more comprehensive understanding of the mechanisms and effects of montane and rainforest biome migrations are needed especially because approximately 71% of plants in the Neotropics comply

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¹ In memoriam.

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with the Andean-centered versus Amazonian-centered view of Gentry (1982).

Palms (Arecaceae) originated in a tropical rainforest-like biome and are considered models to study the evolutionary history of this biome (Couvreur et al., 2011; Baker and Couvreur, 2013; Blach-Overgaard et al., 2013; Eiserhardt et al., 2017). Members of the palm tribe Euterpeae are among the most economically and ecologically important groups of palms. The primary meristem of *Euterpe* Mart., known as “heart of palm,” is consumed fresh or canned and had a world trade volume of 132.6 million US\$ in 2008 (Anonymous, 2009). *Euterpe* fruit (açai) has anti-inflammatory and antioxidant properties (Kang et al., 2012; Odendaal and Schauss, 2014) that have promoted its commercialization in large urban markets worldwide (Brokamp et al., 2011). High quality oil, reminiscent of olive oil in fatty acid composition, is extracted from the fruit mesocarp of several *Oenocarpus* Mart. species (Balick, 1986; Montúfar et al., 2010). The total market value of *Oenocarpus* fruit for human consumption and cosmetics was estimated at 115.92 US\$/ha/year (Pyhälä et al., 2006). Lastly, American indigenous people elaborate baskets, walls, roof thatch, and medicine from the Euterpeae, contributing to their subsistence economy.

The tribe is also an important structural component of Amazonian rain forests. Some species, like *E. precatoria* Mart., *E. oleracea* Mart., and *O. bataua* Mart., are among the 10 most abundant species with diameter at breast height higher than 10 cm in Amazonia (ter Steege et al., 2013). The tribe is restricted to the Neotropics, distributed from Central America to Southeastern Brazil and Bolivia, including the Caribbean islands. Species grow in a wide elevation range, from sea level to 2500 m of elevation (m), and are found in a wide diversity of habitats (Dransfield et al., 2008). The montane and lowland rainforests are the preferred biomes of Euterpeae but the role of biome shifts on species diversification has not been analyzed.

The Euterpeae belongs to the largest palm subfamily Arecoideae, and comprises 33 species in five genera (Fig. 1; *Euterpe*, *Hyospathe* Mart., *Neonicholsonia* Dammer, *Oenocarpus*, and *Prestoea* Hook.f.). Henderson (1999) identified four synapomorphies for the tribe: (1) presence of an ocrea (an extension of the leaf sheath), (2) inflorescences branched to one order or spicate, (3) purple-black fruit, and (4) a crustaceous endocarp. Other features of the tribe include fruits with stigmatic remains and a smooth epicarp (Dransfield et al., 2008). Table S1 describes the synapomorphies or character combinations useful to identify each genus, their geographic distribution, and species number. A sixth genus, *Jessenia* H. Karst., is monotypic and taxonomically controversial. *Jessenia* was separated from *Oenocarpus* based on the presence of flowers with 9–20 stamens in contrast to six in *Oenocarpus*, the presence of a ruminant endocarp instead of homogeneous, having bifid eophyls instead of 4-blade eophyls, the presence of sicklelike trichomes on the abaxial side of the pinnae, and different patterns of flavonoid components (Burret, 1928; Balick, 1986; Bernal et al., 1991). The taxonomic recognition and rank of *Prestoea* and *Euterpe* has also been controversial (Table S2). Some authors had recognized *Prestoea* within *Euterpe* based on overlapping morphological characters such as fruit with subapical to lateral stigmatic remains (Burret, 1929; Wessels Boer, 1965).

Monographs or taxonomic treatments are available for every genus (e.g., Burret, 1928, 1929; Balick, 1986; Skov and Balslev, 1989; Bernal et al., 1991; Henderson and Galeano, 1996; Henderson, 2004). Despite the economic and ecological importance of the tribe, there is no species-level, taxonomically complete, and highly resolved phylogeny. Henderson (1999) conducted a phylogenetic study of the tribe based on 54 morphological and anatomical characters. His maximum parsimony analysis, however, did not provide a measurement of branch support. Subsequently, Montúfar and Pintaud (2008) reconstructed a phylogenetic tree for only 36% of species using four chloroplast intergenic spacers. Intergeneric relationships, however, were not recovered and the tree had an overall low resolution because of the very low number of informative characters (1.5%).

Besides biome shifts, inflorescence type may have also influenced the diversification of Euterpeae through the different pollinators they attract. Some species of *Euterpe* have a tendency for rachillae (i.e., inflorescence branches) to be absent in the adaxial side of the main inflorescence axis, a tendency that is further developed in *Oenocarpus*, where the inflorescence is hippuriform (i.e., resembles the shape of a horsetail) with long and pendulous rachillae (Fig. 1). Balick (1986) proposed that the inflorescence of *Oenocarpus* is derived from an inflorescence with rachillae all around the main axis as in most species of *Euterpe*, through the loss of the adaxial rachillae. His hypothesis was based on the observation of triangular bracts on the place where aborted rachillae would occur. *Oenocarpus* is pollinated almost exclusively by the Curculionidae beetle family (Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al., 2015), and therefore has the most specialized pollination system in the tribe. The remaining Euterpeae genera are pollinated by a range of insect families within orders Coleoptera, Hymenoptera, and Diptera (Ervik and Feil, 1997; Kúchmeister et al., 1997; Listabarth, 2001), displaying a more generalist pollination. It has been shown that transitions to specialized pollination systems are associated with increased diversification rates (e.g., Givnish et al., 2014; Serrano-Serrano et al., 2017; Tripp and Tsai, 2017). We evaluate this hypothesis in the Euterpeae.

Our aim was to provide a robust dated molecular phylogenetic hypothesis of tribe Euterpeae using combined chloroplast and nuclear sequence data with the most comprehensive species sampling to date. We inferred the tribe’s biogeographic history through an ancestral range analysis, and reconstructed ancestral states for inflorescence type and biome occupation. We also inferred whether inflorescence type and biome could be correlated with diversification rates in Euterpeae. Our results were used to: (1) verify the monophyly of tribe Euterpeae and its genera and elucidate intergeneric relationships; (2) interpret ancestral distribution and migration events among biogeographic areas in the light of the Cenozoic geological events that shaped the Neotropics; (3) test Balick’s hypothesis on the evolution of the hippuriform inflorescence; (4) test the hypothesis that the hippuriform inflorescence with specialized beetle pollination is associated with higher diversification rates compared to all other inflorescence types with generalized pollination; and (5) test the hypothesis that the lowland rainforest biome allowed for greater diversification than the montane biome because palms are pre-adapted to the former.

2. Methods

2.1. Sampling

We sampled 27 of the 33 species in Euterpeae including seven infra-specific taxa, thus achieving 81.8% taxon sampling. We used 33 Euterpeae samples from which we obtained 149 new sequences, and 103 new sequences from the 41 species we used as outgroup. Outgroup was chosen from all major tribes in subfamily Arecoideae, but also from subfamilies Ceroxyloideae and Coryphoideae. Since there are no fossils available for calibration within Euterpeae we sampled extensively throughout other palm tribes and subfamilies. Samples were obtained from botanical gardens, herbaria, fieldwork, and donations from palm specialists. The complete list of DNA samples, herbarium voucher information, and genbank numbers are reported in Table S3.

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from silica dried leaves and herbarium specimens using a modified protocol of the Qiagen DNeasy Plant Mini Kit (Germany). Changes in the procedure were as follows: 45 mg of dried leaf material, 600 μ L of Buffer AP1, incubation period of 15 min at 65 $^{\circ}$ C after the addition of Buffer AP1, 195 μ L of Buffer P3, DNA eluted in 50 μ L of Buffer AE, and incubation period of 10 min at room temperature before the final centrifugation step.

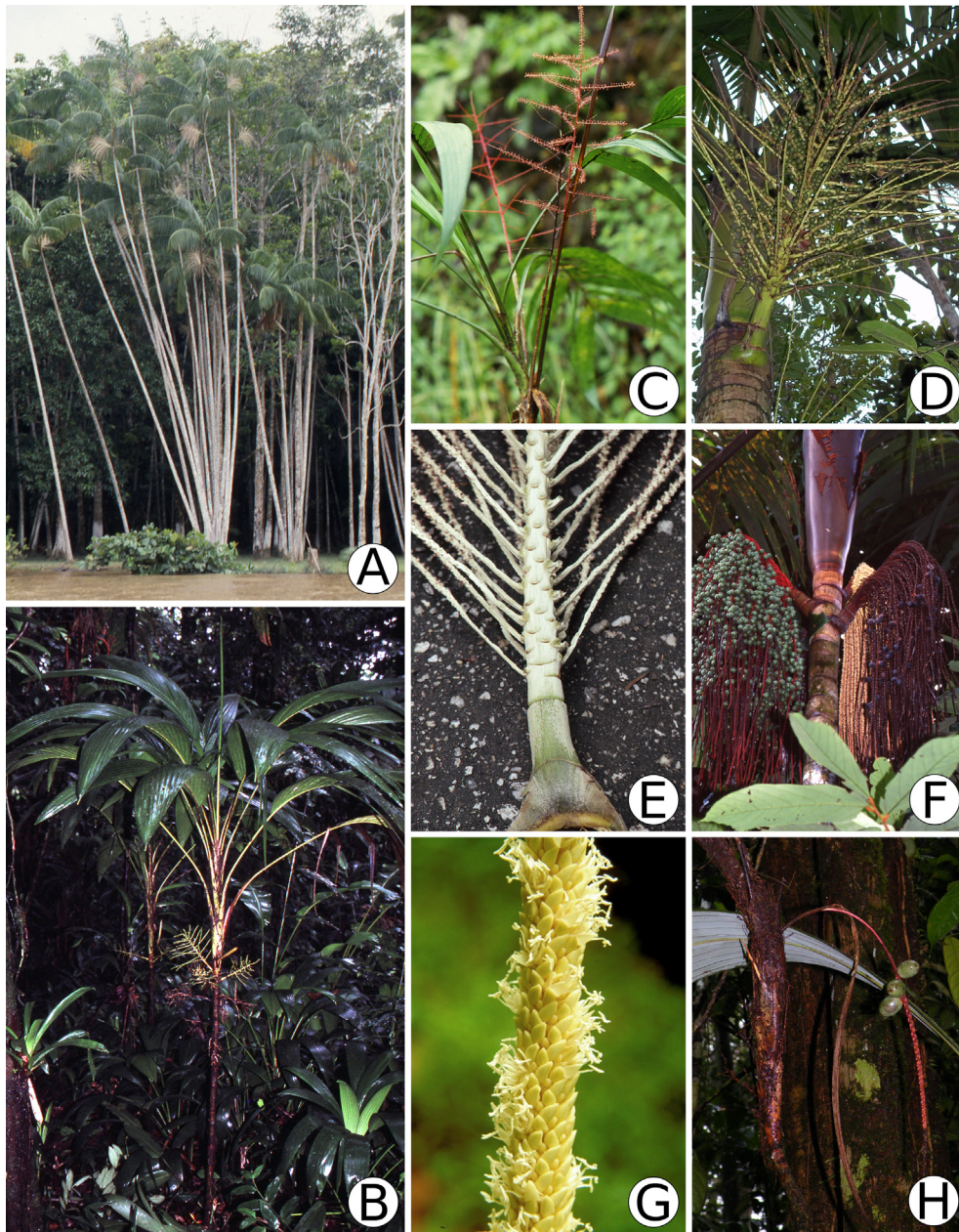


Fig. 1. Growth forms and inflorescence types in Euterpeae. Growth forms: A. Tall and multi-stemmed palm *Euterpe oleracea*; B. small understory palm *Prestoea pubigera*. Inflorescences: C. *Hyospathes macrorhachis* and D. *Prestoea acuminata* var. *montana*, showing inflorescences with rachillae all around the rachis; E. *Euterpe broadwayi* with partial loss of adaxial rachillae; F. hippuriform inflorescence of *Oenocarpus mapora*, showing a complete loss of adaxial rachillae. Non-branching (spicate) inflorescences of G. *Neonicholsonia watsonii* and H. *Oenocarpus simplex*. Photos by Andrew Henderson, Rodrigo Bernal, and Fritz Pichardo-Marcano.

We selected four low-copy nuclear markers and one chloroplast DNA region for phylogeny reconstruction: intron 4 of RNA polymerase II subunit 2 (RPB2; Roncal et al., 2005), a region amplified by the conserved intron-scanning primer set number 4 (CISP4; Bacon et al., 2008), partial exon 1 of phytochrome B (PHYB; Ludeña et al., 2011), WRKY transcription factor 6 (WRKY6; Meerow et al., 2009), and a chloroplast intergenic-spacer (*trnT-trnD*; Demesure et al., 1995). We chose these five DNA regions because they have provided good resolution in previous palm phylogenetic studies. Primers are detailed in Table S4.

The Qiagen Top Taq Master Mix Kit (Qiagen Inc, Valencia, CA, USA) was used to amplify the chosen DNA regions. Amplifications were performed on a 25 μ L solution containing 12.5 μ L of the TopTaq Master Mix 2x, 0.4 μ M of each primer, and ca. 60 ng of the template DNA. When the amplification was unsuccessful with the Qiagen kit, we used

the Epicentre Failsafe PCR Premix Kit (Madison, WI, USA). We prepared a 25 μ L solution with 12.5 μ L of Failsafe Buffer E 2x, 0.4 μ M of each primer, 0.25 μ L of the Failsafe PCR enzyme mix (0.625 Units), and ca. 60 ng of the template DNA. Polymerase chain reaction (PCR) conditions followed the publications for each primer pair. PCR product sizes and annealing temperatures are found in Table S4. We could not obtain RPB2 amplifications for most *Euterpe* species. Only *Euterpe broadwayi* Becc. ex Broadway was successfully amplified when we performed a two-step nested PCR following Roncal et al. (2005) and the Epicentre Failsafe Kit.

PCR products were purified using the Qiagen QIAquick Plant Purification Kit (Qiagen Inc, Valencia, CA, USA) before being sent for Sanger sequencing to Eurofins Genomics (Germany, <https://www.eurofinsgenomics.eu/>) and the Centre for Applied Genomics at the Hospital for Sick Children (Canada, <http://www.tcag.ca/>). The

Table 1

Fossil and secondary calibration points used to date the molecular phylogenetic tree of tribe Euterpeae. Parameter settings used in BEAUti 2.4.4. Mya = million years ago.

Number	Fossil name	Calibrated node	Hard lower bound (Mya)	Soft upper bound 95% (Mya)	Exponential mean (uncertainty)
I	<i>Sabalites carolinensis</i>	stem of subfamily Coryphoideae	84	90	2
II	<i>Echimonoporopollis grandiporus</i>	stem of <i>Ravenea</i>	41.2	65.2	8
III	<i>Socratea brownii</i>	stem of <i>Socratea</i>	22.5	31.5	3
IV	<i>Tripylocarpa aestuaria</i>	stem of subtribe Attaleinae	61.9	64.9	1
V	<i>Bactris pseudocuesco</i>	crown of subtribe Bactridiinae	26	33.5	2.5
	Secondary calibrations	Calibrated node	Mean	Standard deviation	
VI	Geonomateae	crown of Geonomateae	30.7	4	
VII	Chamaedoreae	crown of Chamaedoreae	50	4.5	

resulting chromatograms were observed, assembled and edited in Geneious 7.1.8 (<https://www.geneious.com>, Kearse et al., 2012). IUPAC codes were used to treat heterozygotes. Sequences for each molecular marker were aligned individually with MAFFT 7.271 (Katoh and Standley, 2013). Alignments were later manually refined to get a total concatenated DNA matrix consisting of 5476 aligned positions and ca. 10% missing data.

2.3. Phylogenetic analyses

We used two model-based methods to reconstruct the phylogenetic relationships of tribe Euterpeae. A maximum likelihood (ML) analysis was conducted in RAxML 8.2.4. (Stamatakis, 2014), and a Bayesian inference (BI) was carried out in BEAST 2.4.4 (Bouckaert et al., 2014).

RAxML was run with the GTR + G nucleotide substitution model because the choice of substitution models in RAxML is limited to parameter rich models of the GTR family, and the RAxML user manual discourages the use of the proportion of invariable sites (+I parameter). Furthermore, the Bayesian information criterion in jModeltest2 (Darriba et al., 2012) implemented in the CIPRES Science Gateway 3.3 (Miller et al., 2010) supported the +G parameter for all DNA regions. We performed 1000 rapid bootstrap replicates to assess branch support, and a thorough ML search following Stamatakis (2014). For the BI, the best nucleotide substitution model was selected for each DNA marker using jModeltest2. The TPM1uf + G model of sequence evolution was selected for *trnD-trnT*, the TPM3uf + G model for CISP4 and RPB2; and HKY + G was selected for WRKY6 and PHYB. We used a birth-death tree model without specifying a starting tree (random). We set monophyly priors for subfamily Coryphoideae, and for the clade Ceroyloideae + Arecoideae in BEAST as the monophyly of these groups is well supported (Baker et al., 2009; Faurby et al., 2016). We used two runs of a Markov chain Monte Carlo (MCMC) chain length of 30 million generations sampling every 3000 trees.

We verified that the MCMC runs had reached convergence using Tracer 1.7 (Rambaut et al., 2018), and by ensuring that all effective sample sizes exceeded 200. Tree and log files were combined with Log Combiner 2.4.4 (Bouckaert et al., 2014). Following the removal of 25% burn-in, the remaining 15,002 sampled posterior trees were summarized using Tree Annotator 2.4.4 (Bouckaert et al., 2014) to generate a maximum clade credibility (MCC) tree and calculate the posterior probabilities (pp) as branch support estimates. We visualized ML and BI trees in FigTree 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>).

2.4. Divergence time estimation

To obtain a chronogram we used the BEAST 2.4.4 settings as described before with an uncorrelated log normal relaxed molecular clock model, and TreeAnnotator 2.4.4 to calculate the mean and median ages, and 95% highest posterior density intervals (95% HPD). We selected seven calibration points. Five of these were fossils carefully selected according to the five criteria proposed as best practices for justifying fossil calibrations (Parham et al., 2012). In addition, we used two

secondary calibration points obtained from the literature.

Because of the lack of reliable fossils within the study group, we searched for fossils in other tribes of Arecoideae. The fossil record of tribe Cocoseae is abundant and reliable; thus two fossils were used to calibrate nodes within Cocoseae: (1) *Bactris pseudocuesco* from the Middle Oligocene of Puerto Rico (Collazo Shale Formation). Hollick (1928) noted that the fossilized fruits of this sample resembled those of the extant *Bactris cuesco*. (2) *Tripylocarpa aestuaria* from the late Danian of Argentina (Salamanca Formation). This fossilized fruit shows mesocarp with furrows or striations and three distinctive longitudinal markings running from apex to base of the epicarp, similar to Attaleinae (Futey et al., 2012). From the tribe Iriarteae we used (3) *Socratea brownii* from the Late Oligocene of Mexico (Quinta Formation). The fossil is composed of staminate flowers preserved in amber with morphological characters and stamen number similar to *Socratea* (Poinar, 2002).

Outside Arecoideae we selected two fossils as representatives of subfamilies Ceroyloideae and Coryphoideae: (4) *Echimonoporopollis grandiporus* pollen fossil from Lower to Middle Eocene of India (Neyveli Formation; Saxena et al., 1992), for which Harley (2006) found a resemblance with pollen of *Ravenea* in subfamily Ceroyloideae; and (5) *Sabalites carolinensis* from the late Coniacian to early Santonian of the United States of America. This fossil consists of impressions of a fan palm with very flabellate leaves and numerous rays that resemble those of subfamily Coryphoideae (Berry, 1914). This last fossil served also to calibrate the root of the tree. The two secondary calibration points were: (6) the crown age of tribe Geonomateae as estimated in Roncal et al. (2010); and (7) the crown age of tribe Chamaedoreae based on the work of Cuenca et al. (2008). Table 1 shows the settings used in BEAST and the position of the seven calibrated nodes in the tree. We used exponential distributions for the fossil calibrations and normal distributions for the secondary calibrations, following the recommendations of Ho and Phillips (2009). Matrices and trees were submitted to TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S23200>).

2.5. Biogeographical analyses

We defined seven biogeographical areas based on the geological history of the Neotropics and the current distribution of tribes Euterpeae and Areceae. These were: (A) Central America and Chocó; (B) Caribbean; (C) Andes; (D) Amazonia; (E) Guiana Shield; (F) Brazilian Atlantic Forest; and (G) Indo-Pacific region. We delimited these biogeographical areas using The Nature Conservancy (2009) terrestrial ecoregions of the world. We coded a distribution matrix in presence-absence format for each taxon on each of the seven biogeographic areas (Table S5) based on verified data available at The Global Biodiversity Facility (GBIF, <https://www.gbif.org/>), expert maps, taxonomic revisions, and species identification guides (Henderson et al., 1995; Henderson and Galeano, 1996; Borchsenius et al., 1998; Henderson, 2004; Galeano and Bernal, 2010; Lorenzi et al., 2010).

To infer the biogeographical history of the Euterpeae we performed

an ancestral range estimation analysis using maximum likelihood with the R package 'BioGeoBEARS' 0.2.1 (Matzke, 2013). For this analysis we used an outgroup-reduced version of the dated Bayesian phylogenetic tree comprising only tribes Euterpeae and Areceae (the sister tribe, see results Section 3.1). BioGeoBEARS implements commonly used models of range evolution such as dispersal, extinction, cladogenesis (DEC), BAYAREALIKE, and DIVALIKE. It also implements a jump parameter +J to each of them, which adds a founder-event parameter to the models. For each of these six range evolution models, we tested three biogeographic models, which enforce different dispersal probabilities among areas throughout different time periods. Therefore, a total of eighteen models were compared using the Akaike information criterion (AIC, Akaike, 1974) in BioGeoBEARS. The inferred ancestor was constrained to a maximum of four areas since this was the maximum number of areas that any Euterpeae species occupies.

We defined a 'null' biogeographic model with equal probability of dispersal among all biogeographic areas through time (values of 1). For the 'complex biogeographic models 1 and 2', we stratified the evolutionary history of Euterpeae into four and six time frames, respectively, and elaborated a dispersal cost matrix for each one of them, reflecting the American palaeogeographical history during the last 47 million years (Table S6). Throughout the first time frame (0–10 Mya), the Andes achieved their maximum elevation and thus could have acted as a dispersal barrier (Gregory-Wodzicki, 2000). The second time frame (10–15 Mya) was characterized by the closure of the Panamanian Isthmus, and the Andes had already risen up to approximately half of their current elevation (Gregory-Wodzicki, 2000; Montes et al., 2015). During the third time frame (15–20 Mya), the Panama Isthmus was open diminishing the potential of crossing between Central and South America; the Andes also achieved around half their current elevation (Gregory-Wodzicki, 2000; Montes et al., 2015). In the course of the fourth time frame (20–47 Mya), the Central and northern Andes did not have an elevation that would impede movement of taxa across or into these lands (Gregory-Wodzicki, 2000), and there was no landmass uniting Central and South America (Montes et al., 2015). For the 'complex biogeographic model 2' we used a six-time partition. We used the same time periods as in the 'complex biogeographic model 1' and included a new time frame (33–35 Mya), when a controversial land bridge called GAARlandia existed (Iturralde-Vinent and MacPhee, 1999) and would have facilitated the movement of taxa between Central and South America (Table S6).

Dispersal values closer to 0 represent a greater dispersal penalty, and a value of 1 was assigned to adjacent areas with no dispersal barriers (e.g., mountains, water). We imposed a dispersal value of 0.5 to non-adjacent areas separated by two steps and no other dispersal constraints, or to dispersal from the Andes to adjacent areas or vice-versa, between 10 and 20 Mya (when the Andes were at half their current elevation). A value of 0.33 was attributed to dispersal between non-adjacent areas separated by three or more steps and no other dispersal constraint. A dispersal constraint of 0.33 was also assigned for the dispersal between the Andes and adjacent areas between 0 and 10 Mya

(Andes at current elevation), or the dispersal across the Andes between 10 and 20 Mya. A value of 0.1 was imposed for areas that lacked land connectivity, taxa must have therefore dispersed across the water; and for the dispersal across the fully formed Andes between 0 and 10 Mya. Lastly, we imposed a value of 0.01 for the dispersal to or from the Indo-Pacific Region (Table S6).

2.6. Inflorescence evolution, biome shifts, and their association with diversification rate

We reconstructed the evolution of the inflorescence branching pattern and biome occupation in Euterpeae using a maximum likelihood approach with the function 'rayDISC' of the 'corHMM' package 1.22 (Beaulieu et al., 2015). The 'rayDISC' function allows coding polymorphic taxa. We defined four inflorescence character states based on the literature (Balick, 1986; Bernal et al., 1991; Henderson and Galeano, 1996; Henderson, 2004; Dransfield et al., 2008): (1) inflorescence with rachillae all around the main axis; (2) inflorescence with a partial loss of adaxial rachillae; (3) inflorescence with a complete loss of adaxial rachillae (hippuriform); and (4) unbranched inflorescence (spicate). The Euterpeae occupies the montane and lowland tropical rainforest biomes in the Neotropics with several species growing on both (Table S5; Henderson et al., 1995; Henderson and Galeano, 1996). Based on the distribution of Euterpeae species we used a threshold value of 1000 m above sea level (masl) to distinguish these two biomes. We used the literature cited above to score a matrix of taxon vs. inflorescence type and taxon vs. biome occupation for each member of the Euterpeae + Areceae clade. The ancestral state at each node was reconstructed on the outgroup-reduced version of the dated Bayesian phylogenetic tree. Data were tested under three different predefined character state transition rates models: (1) ER (equal rates model); (2) SYM (symmetrical rates model); and (3) ARD (all rates different model). The likelihood value and AIC score for each model were compared.

To test our hypotheses on the association of inflorescence type and biome with diversification rates, we implemented the Binary State Speciation and Extinction model (BiSSE) (Maddison et al., 2007) using the R package Diversitree 0.9.10 (FitzJohn, 2012). BiSSE estimates speciation and extinction rates among lineages with different states of a binary trait. For the inflorescence-associated diversification analysis, we coded taxa as having a hippuriform versus non-hippuriform inflorescence using the clade of all Euterpeae genera except *Hyospathe*. We used this smaller clade since states represented in < 25% of the taxa do not have the statistical power to confidently reveal diversification rate differences (Maddison and FitzJohn, 2015). We used the outgroup-reduced version of the dated Bayesian tree for the biome diversification analysis. To account for missing taxa, we applied a sampling fraction that varied by state (FitzJohn et al., 2009). These fractions were 0.71 for lowland rainforest taxa, 0.55 for montane taxa, 0.46 for taxa with non-hippuriform inflorescence, and 0.67 for taxa with hippuriform inflorescence. We compared eight models (Tables 2 and 3) of increasing

Table 2

Model comparison for the BiSSE analyses of inflorescence correlated diversification (0 = non-hippuriform, 1 = hippuriform), with parameter estimates for each model without taxonomic sampling correction. The best-fitting model as determined by the lowest Akaike information criterion (AIC) and highest AIC weight is highlighted in bold. λ = speciation rate; μ = extinction rate; q = transition rate; Df = degrees of freedom.

Models	λ_0	λ_1	μ_0	μ_1	q_{01}	q_{10}	Df	lnLik	AIC	AICw
full ($\lambda_0 \neq \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} \neq q_{10}$)	0.279	0.215	0.226	0.258	0.049	< 0.01	6	-70.533	153.07	0.037781
equal l ($\lambda_0 = \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} \neq q_{10}$)	0.25	0.25	0.185	0.297	0.058	< 0.01	5	-70.592	151.18	0.097203
equal m ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} \neq q_{10}$)	0.29	0.205	0.243	0.243	0.045	< 0.01	5	-70.542	151.08	0.102187
equal q ($\lambda_0 = \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} = q_{10}$)	0.3	0.185	0.265	0.17	0.032	0.032	5	-71.173	152.34	0.054424
equal lm ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} \neq q_{10}$)	0.244	0.244	0.213	0.213	0.035	< 0.01	4	-70.999	150	0.175354
equal lq ($\lambda_0 = \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} = q_{10}$)	0.244	0.244	0.206	0.221	0.035	0.035	4	-71.45	150.9	0.111811
equal mq ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} = q_{10}$)	0.255	0.221	0.208	0.208	0.035	0.035	4	-71.34	150.68	0.124812
equal lmq ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} = q_{10}$)	0.244	0.244	0.213	0.213	0.035	0.035	3	-71.475	148.95	0.296428

Table 3

Model comparison for the BiSSE analyses of biome correlated diversification (0 = lowland rainforest, 1 = montane), with parameter estimates for each model without taxonomic sampling correction. The best-fitting model as determined by the lowest Akaike information criterion (AIC) and highest AIC weight is highlighted in bold. λ = speciation rate; μ = extinction rate; q = transition rate; Df = degrees of freedom.

Models	λ_0	λ_1	μ_0	μ_1	q_{01}	q_{10}	Df	lnLik	AIC	AICw
full ($\lambda_0 \neq \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} \neq q_{10}$)	0.105	0.252	0.088	0.207	0.019	0.061	6	-128.01	268.02	0.096131
equal l ($\lambda_0 = \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} \neq q_{10}$)	0.167	0.167	0.249	< 0.01	< 0.01	0.17	5	-128.71	267.42	0.129764
equal m ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} \neq q_{10}$)	0.113	0.228	0.139	0.139	0.012	0.1	5	-128.11	266.23	0.235266
equal q ($\lambda_0 \neq \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} = q_{10}$)	0.092	0.307	0.041	0.298	0.033	0.033	5	-128.25	266.51	0.20453
equal lm ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} \neq q_{10}$)	0.145	0.145	0.114	0.114	0.018	0.067	4	-129.46	266.92	0.16662
equal lq ($\lambda_0 = \lambda_1$; $\mu_0 \neq \mu_1$; $q_{01} = q_{10}$)	0.147	0.147	0.103	0.168	0.029	0.029	4	-130.74	269.48	0.046327
equal mq ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} = q_{10}$)	0.09	0.181	0.049	0.049	0.012	0.012	4	-130.71	269.41	0.047977
equal lmq ($\lambda_0 = \lambda_1$; $\mu_0 = \mu_1$; $q_{01} = q_{10}$)	0.145	0.145	0.114	0.114	0.017	0.017	3	-131.28	268.56	0.073385

complexity in which speciation, extinction and transition rates were modeled to vary or remain equal between states. Fit of all models was compared using AIC scores. We also ran BiSSE using MCMC estimations for 10,000 generations based on an unconstrained model (full). The resulting distribution of estimated speciation and extinction rates were plotted with a helper function in Diversitree. In addition, to test the effect of our sampling correction function, we ran all BiSSE analyses assuming a taxonomically complete phylogeny.

3. Results

3.1. Phylogenetic relationships

PHYB DNA region was removed from the concatenated phylogenetic analyses due to a very strong discrepancy in the phylogenetic signal with other DNA markers. The genus *Hyospathe* and some *Prestoea* taxa formed a strongly supported clade with tribe Geonomateae in the PHYB gene tree (Fig. S1). Incomplete lineage sorting at the PHYB locus or hybridization are potential explanations for this phylogenetic conflict. The final concatenated 74-accession dataset contained 4593 aligned positions.

Both ML and BI concatenated analyses recovered congruent topologies within Euterpeae and the outgroup (Figs. 2 and S2). The Euterpeae was monophyletic (0.97 pp, 100% bootstrap support (BS)) and was sister to tribe Areceae (0.96 pp, 96% BS). All genera within Euterpeae were monophyletic, and all intergeneric relationships were recovered with high support. *Hyospathe* was recovered as sister to all other genera (0.98 pp, 100% BS). *Oenocarpus* was supported as sister to *Prestoea* (0.97 pp, 73% BS) and *Euterpe* as sister to the monotypic genus *Neonicholsonia* (0.98 pp, 100% BS, Fig. 2).

Most of the interspecific relationships were resolved with good support (> 0.95 pp, > 90% BS), especially for *Hyospathe* and *Euterpe*. The tropical rainforest widespread species *Euterpe precatoria* and *Hyospathe elegans* Mart. were polyphyletic, and *Prestoea acuminata* (Willd.) H.E.Moore was paraphyletic. Within *Prestoea*, the analyses recovered two main clades with good support (> 0.97 pp, > 99% BS). One consisted of five species distributed in mostly montane habitats (usually from 1000 to 2000 m), and the second consisted of three species distributed in lowland tropical rainforests (from 0 up to 900 m). In *Oenocarpus*, the widely distributed *O. bataua* was recovered as sister to all other *Oenocarpus* species sampled (Fig. 2).

3.2. Divergence times

Mean and median node ages slightly differed (Table 4). Therefore, we refer to mean node ages for divergence times hereafter. Based on the analysis in BEAST the mean crown age for Euterpeae was 39.18 Mya (95% HPD 32.22–48.4), and the mean stem age was 45.28 Mya (95% HPD 38.97–54.65). Euterpeae diverged from Areceae during the Eocene but cladogenesis within the extant genera of Euterpeae began around 10 Mya and extended into the Pliocene and Pleistocene. The monotypic

Neonicholsonia diverged first at around 20 Mya. *Hyospathe*, *Prestoea*, and *Euterpe* had concurrent most recent common ancestors (MRCA) at around 10 Mya. *Oenocarpus* had the most recent crown age among all Euterpeae genera at around 7 Mya. Fig. 3 and Table 4 show the divergence times for 30 nodes of interest and their confidence intervals (95% HPD).

3.3. Biogeographical analyses

The AIC values showed that the DEC range evolution model under the ‘complex biogeographical model 1’ was the best-fit model for our data set (Table S7). The use of parameter *j* (founder-event speciation) did not improve the fit of the DEC model, and all null models (no dispersal constraints) fit our data poorly (Table S7).

Central America-Chocó was the most likely inherited ancestral range for the Euterpeae, although there was much uncertainty in this reconstruction (Fig. 4, Table 4). Considering only the ancestral area that received the highest probability at each node, four independent colonization events from Central to South America were recovered. The first was by the ancestor of *Hyospathe* between 40 and 10 Mya to a wide area in Amazonia, the Andes, and the Guiana Shield. Subsequently, diversification in the Andes was evidenced in *Hyospathe* with most divergence occurring in the last 7 million years. The second event was by the ancestor of *Oenocarpus* between 21 and 7 Mya, migrating from Central America to Amazonia, and a final expansion of this genus to the Guiana Shield 1 Mya. The third colonization event to South America, and more specifically to the Andes, was found in the ancestor of the montane *Prestoea* clade at around 9–5 Mya. A subsequent expansion occurred into the Guiana Shield and the Caribbean between 5 and 2 Mya. Divergence of the Caribbean endemic *P. acuminata* var. *montana* (Graham) A.J. Hend. & Galeano occurred at around 1 Mya (95% HPD 0.06–1.59). Lastly, colonization to South America (broadly Andes, Amazonia, Guiana Shield, and Atlantic forest) occurred in the ancestor of *Euterpe* between 20 and 10 Mya (Fig. 4). Divergence of the Caribbean endemic *E. broadwayi* occurred later at ca. 2.2 Mya (95% HPD 0.05–4.0). *Neonicholsonia* evolved in Central America and did not migrate to South America. Colonization of the Brazilian Atlantic forest from Amazonia occurred at a minimum age of ca. 1.38 Mya (95%HPD 0.0–2.84).

3.4. Inflorescence evolution, biome shifts, and their association with diversification rates

We chose the simplest ER model to reconstruct the ancestral inflorescence type and biome in Euterpeae since it received the lowest AIC scores. The analysis suggested that the ancestral inflorescence branching pattern in Euterpeae was an inflorescence with rachillae distributed all around the main axis (Fig. 5). From this ancestral state, the analysis recovered four shifts to different inflorescence types. One shift was a complete loss of adaxial rachillae (hippuriform inflorescence) as seen in *Oenocarpus*. One shift to an inflorescence with

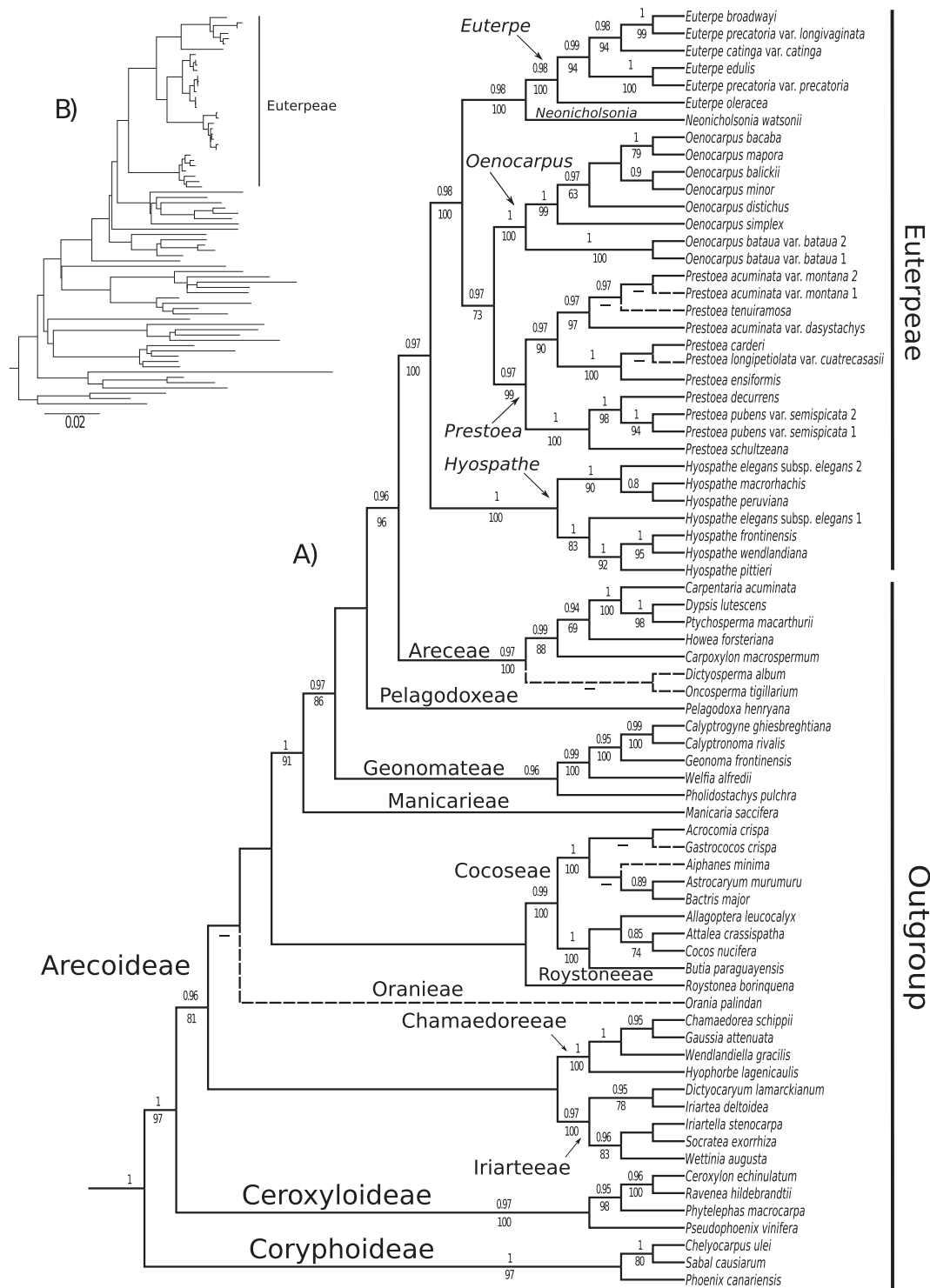


Fig. 2. A Bayesian maximum clade credibility tree of tribe Euterpeae and outgroup resulting from the combined analysis of three nuclear and one chloroplast DNA markers. Values above the branches are the Bayesian posterior probabilities (pp > 0.8), and values below are the maximum likelihood bootstrap values (BS > 60). Dashed lines depict relationships that were not recovered in the maximum likelihood tree. B. Maximum likelihood phylogram showing branch lengths.

partial loss of adaxial rachillae in the ancestor of *Euterpe*. Two shifts to a spicate (unbranched) inflorescence type were recovered: one in *Neonicholsonia* and the other in *Oenocarpus simplex* R.Bernal, Galeano & A.J. Hend. (Fig. 5). The biome occupied by the ancestor of tribe Euterpeae was the lowland rainforest. From this ancestral state, the analysis recovered two main shifts to the montane biome: one in the ancestor of *Hyospathe*, and the other in the ancestor of the Andean *Prestoea* clade (Fig. 5).

The AIC scores from BiSSE analyses recovered equal lmq as the best-fit diversification model for inflorescence type (Table 2), suggesting an equal speciation, extinction and transition rates between taxa with hippuriform and non-hippuriform inflorescences. However, for the biome BiSSE analysis, the equal m was the best-fit model. Speciation rates were twice as higher for the montane than for the lowland rainforest taxa ($\lambda_0 = 0.113$, $\lambda_1 = 0.228$, Table 3). The posterior density of the parameters λ (speciation) was different between biomes but not

Table 4

Divergence times and ancestral area probabilities for tagged nodes in Figs. 3 and 5. HPD = highest posterior density. Biogeographic areas: A = Central America and Chocó, B = Caribbean, C = Andes, D = Amazonia, E = Guiana Shield, F = Atlantic Forest, G = Indo-Pacific. We show ancestral biogeographic ranges with a probability above 0.10. N/A = not applicable.

Node number	Node name	Mean node age	Median node age	95% HPD	Ancestral biogeographic range probabilities
1	Crown of Euterpeae	39.18	40.23	32.22–48.4	A:0.14; ACDE:0.11
2	Crown of Hyospathe	9.34	9.31	5.72–14.7	CDE:0.41; C:0.19; CD:0.13
3	Clade within Hyospathe	6.19	6.13	2.95–10.44	C:0.37; CDE:0.32; CD:0.14
4	Clade within Hyospathe	6.77	6.73	3.66–11.1	C:0.42; CDE:0.28; CD:0.13
5	Sister clade to Hyospathe	28.45	29.03	21.91–36.61	A:0.59
6	Prestoea and Oenocarpus clade	21.16	21.48	14.88–29.16	A:0.48
7	Crown of Prestoea	9.25	9.11	5.49–13.88	A:0.40; ABCE:0.17
8	Lowland Prestoea	4.04	3.93	1.7–7.26	A:0.81; AD:0.19
9	Montane Prestoea	4.72	4.51	2.25–7.34	C:0.37; BCE:0.16; BC:0.13; CE:0.11
10	<i>P. acuminata</i> and <i>P. tenuiramosa</i> clade	2.27	2.05	0.76–3.82	BCE:0.66; BC:0.18; CE:0.13
11	<i>P. acuminata</i> var. <i>montana</i> and <i>P. tenuiramosa</i> clade	0.86	0.63	0.06–1.59	BE:0.99
12	Crown of Oenocarpus	7.12	7.02	4.01–11.78	D:0.47; DE:0.21; ADE:0.16; AD:0.12
13	Crown of <i>O. bataua</i>	1.17	1.04	0.02–2.47	N/A
14	Sister clade to <i>O. bataua</i>	4.0	3.92	1.91–6.72	D:0.98
15	<i>O. bacaba</i> and <i>O. mapora</i> clade	0.73	0.64	0.0–1.55	DE:0.73; ADE:0.13
16	<i>Euterpe</i> and <i>Neonicholsonia</i> clade	19.53	19.88	13.6–26.84	A:0.61
17	Crown of <i>Euterpe</i>	9.92	9.98	6.23–14.59	CDEF:0.24
18	Sister clade to <i>Euterpe oleracea</i>	8.04	8.04	4.72–12.67	CDEF:0.18
19	<i>E. edulis</i> and <i>E. precatória</i> clade	1.38	1.25	0.0–2.84	CDEF:0.40; ADEF:0.19; ACDF:0.18; ACEF:0.13
20	<i>E. broadwayi</i> - <i>E. precatória</i> - <i>E. catíng</i>	4.1	4.04	1.71–7	ABCD:0.20; CD:0.11
21	Tribe Euterpeae and Areceae clade	45.28	46.42	38.97–54.65	AG:0.15; ACG:0.10
22	Crown of tribe Areceae	33.3	34.28	26.55–42.14	G:1.0
23	Crown of tribe Geonomateae	32.98	33.13	26.68–39.19	N/A
24	Crown of tribe Cocoseae	62.63	62.4	61.9–64.04	N/A
25	Crown of subtribe Bactridiinae	31.14	30.62	26.37–37.58	N/A
26	Crown of subtribe Attaeliinae	28.02	28.2	16.58–43.69	N/A
27	Crown of tribe Chamadoreae	47.73	48.73	39.84–57.21	N/A
28	Crown of tribe Iriarteae	30.01	29.1	24.13–36.2	N/A
29	Crown of subfamily Ceroxyloideae	68.81	69.77	60.01–79.73	N/A
30	Crown of subfamily Coryphoideae	60.14	61.79	36.9–82.23	N/A

between inflorescence types, and the posterior density of parameters μ (extinction) was not different in both cases (Fig. 6). The best-fit model for biome- and inflorescence-associated diversification was the same when the taxonomic sampling correction was used (Table S8). This result suggests that taxonomic sampling does not have an effect on the estimated diversification rates for Euterpeae.

4. Discussion

4.1. Systematics of tribe Euterpeae

The sister relationship of tribes Euterpeae and Areceae shown in our study was previously recovered in studies of subfamily Arecoideae using phylogenomics (Comer et al., 2016). Our analysis resolved all intergeneric relationships with high support. The sister relationship between *Euterpe* and *Neonicholsonia* was not recovered in any other previous phylogenetic reconstruction (Henderson, 1999; Montúfar and Pintaud, 2008; Baker et al., 2009; Faurby et al., 2016). Some previously proposed clades, however, were supported in our study. For example, as shown in the morphology-based phylogenetic tree of Henderson (1999), we recovered *Prestoea* sister to *Oenocarpus*. Henderson (1999) identified characters to support this relationship like transverse veins forming a continuous pattern between longitudinal veins, free sepals on the staminate flowers, fruit mesocarp with a distinctive layer of subepidermal sclerosomes, and a layer of flattened, closely spaced fibers forming a “stockade” around the fruit endocarp. The studies by Baker et al. (2009) and Faurby et al. (2016) recovered *Hyospathe* sister to all other Euterpeae genera as in the present study. *Hyospathe* has some floral characters that are distinctive and unusual in the Areceae, e.g., the difference in length of antesealous and antepetalous stamens, and the adnation of the antepetalous filaments to the pistillode (Dransfield et al., 2008). The intergeneric relationships recovered in the present study support the recognition of *Euterpe* and *Prestoea* as separate

genera. Some infrageneric clades were concordant with those in Henderson (1999), who identified morphological synapomorphies for these clades. For example, the clade of *Euterpe caatinga* Wallace, *E. broadwayi*, and *E. precatória*; the clade of *Prestoea pubens* H.E.Moore, *P. decurrens* H.E.Moore, and *P. schultzeana* (Burret) H.E.Moore; and subgenus *Oenocarpus*.

Oenocarpus bataua, previously *Jessenia bataua* (Mart.) Burret was sister to the rest of the members of the genus, which does not clarify the controversial recognition of *Jessenia* as a separate genus. The discovery of *Oenocarpus* species that share some of the unique characters of *Jessenia*, like the ruminant endosperm (in *O. makeru* R.Bernal, Galeano & A.J.Hend.) and bifid eophyls (in *O. simplex*) weakens the argument of a separate genus (Bernal et al., 1991). We thus consider this taxonomic split unnecessary given the morphological and molecular evidence at hand. Some widely distributed species in the Neotropics were para- or polyphyletic. An increased sampling effort throughout the entire distribution range of these species, and the use of species delimitation methods based on coalescent theory and taking into account gene flow are necessary to unveil new species, resolve species complexes, and infer the full evolutionary history of the Euterpeae.

4.2. Divergence times and historical biogeography of Euterpeae

Chief among fossil selection criteria is the reliability of the taxonomic identity and their placement in the phylogenetic tree. Although the palm family has a rich fossil record, there is no reliable fossil that could be unambiguously identified to belong to Euterpeae. The fossil *Palmaepites eocenica* was first assigned a relationship with *Jessenia* (*Oenocarpus*) or *Juania*. However, Harley (2006), in a review of palm fossils, found the association with either genus was unfounded. Poinar (2002) mentioned a flower fossil found in Mexican amber with a resemblance to *Neonicholsonia*, but could not place this fossil in any extant genus with certainty. Hoorn (1993, 1994) described pollen fossils

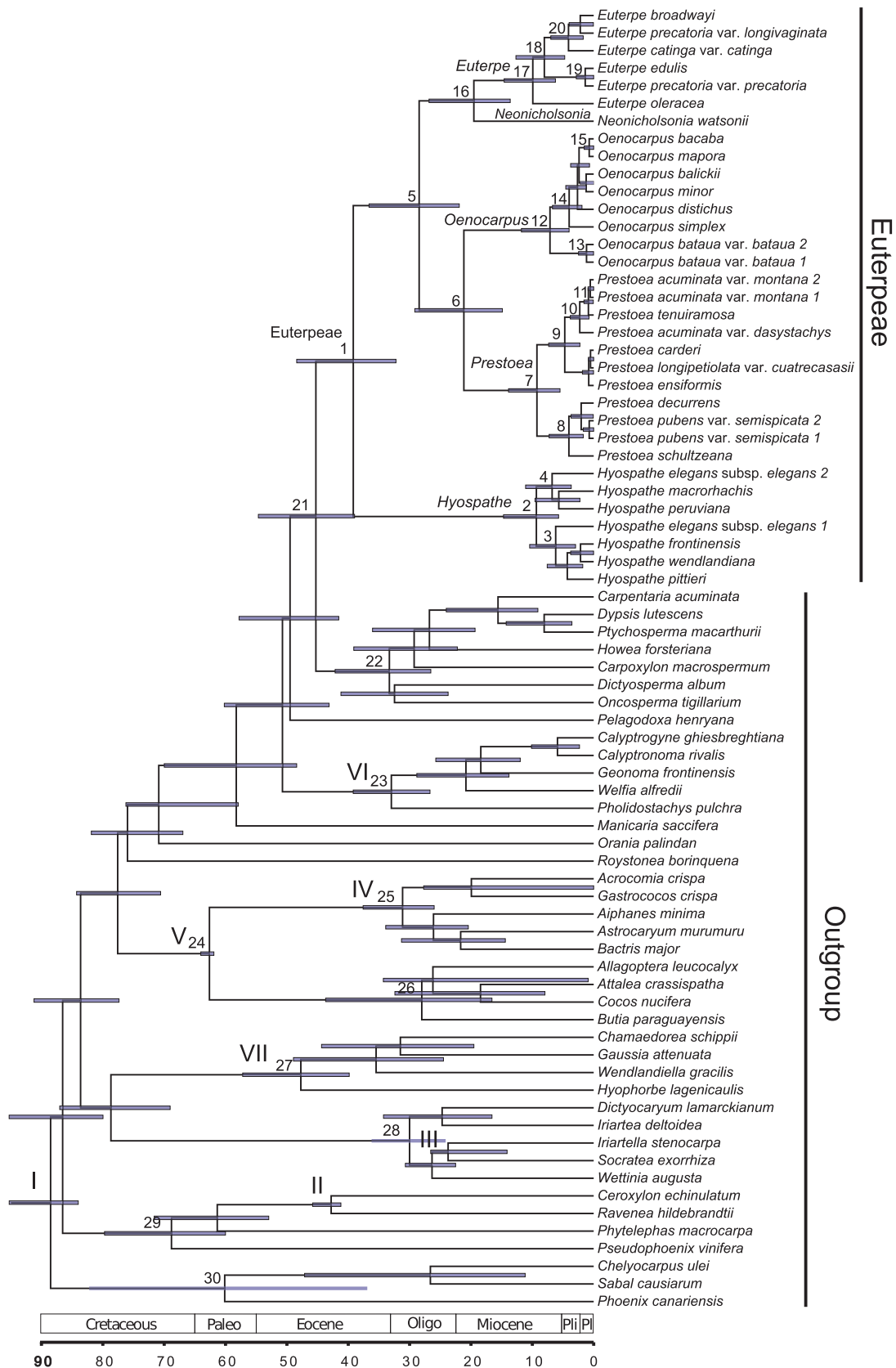


Fig. 3. Chronogram of tribe Euterpeae and outgroup based on the maximum clade credibility tree from the BEAST analysis. Posterior estimates of divergence times were estimated from a partitioned analysis using three nuclear and one chloroplast DNA markers. Blue bars represent the 95% highest posterior densities. Roman numbers represent calibration points (Table 1). Arabic numbers represent nodes of interest (Table 4). Geological time-scale abbreviations: Paleo = Paleocene, Oligo = Oligocene, Plio = Pliocene, Pl = Pleistocene. Bottom scale bar correspond to ages in millions of years.

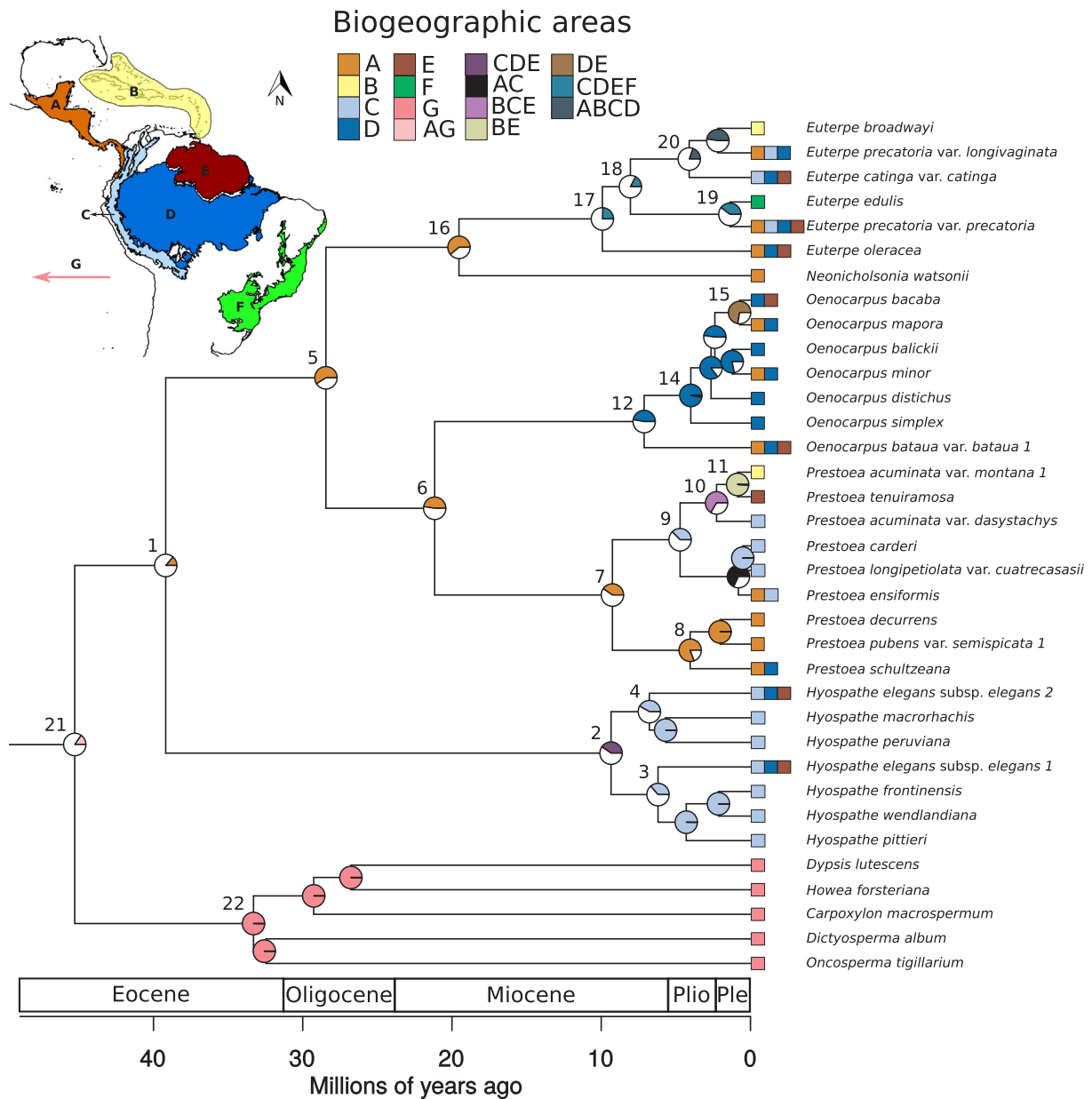


Fig. 4. Ancestral area estimation of tribe Euterpeae using BioGeoBEARS. The colored section of the pies show the most probable distribution for the ancestor at each node and the white section represents the rest of the combined probabilities. Arabic numbers represent nodes of interest (Table 4). Colored squares at the tips indicate the current distribution of each taxon. Inset shows map with biogeographic areas. Geological time-scale abbreviations: Plio = Pliocene, Ple = Pleistocene.

that resemble *Euterpe* (*Psilamonocolpites amazonicus*), and others having an affinity to the palm family more generally (*P. nanus*). In a recent publication, affinities of these fossils were changed without additional data to *Geonoma/Euterpe*, and *Euterpe*, respectively (Salamanca Villegas et al., 2016). Given this confusing history of their taxonomic affinity, we decided not to include these fossils as calibration points.

Our analysis showed that the most probable ancestral area for the Euterpeae was Central America-Chocó. Although this was the best estimation, the probability supporting this hypothesis is low (14%). Internal nodes leading to all genera except *Hyospathe* (nodes 5, 6, 16) show Central America as the most probable ancestral range with higher confidence ($\geq 48\%$), with subsequent colonization events to South America perhaps facilitated by the early formation of the Panama Isthmus (15–13 Mya, Montes et al., 2015). The evolution of the palm family followed a North to South America migration (Baker and Couvreur, 2013), a trend that our results confirm. However, Baker and Couvreur (2013) suggested that the ancestor of Euterpeae was

distributed only in South America, and subsequently expanded to Central America. In this latter scenario, however, it remains difficult to explain the possibility of extinction of most Euterpeae clades in South America (as shown by the absence of South American ancestors in many of the internal nodes; see ancestral reconstructions) and recolonization of the south by the ancestor of extant genera. Tribe Areceae, the sister clade to Euterpeae, is restricted to the Indo-Pacific region. Because of the scale of our analysis no inference could be drawn for the direction of migration but Baker and Couvreur (2013) proposed a long-distance dispersal event from South America to the Indo-Pacific region.

The orogenic events of the Andes left an imprint in the evolutionary history and biogeography of Neotropical plants. Evidence that plants diversified tracking the geological history of the Andes is mounting: *Ceroxylon* (Sanín et al., 2016), Iriarteae (Bacon et al., 2018), Lobeioideae (Lagomarsino et al., 2016), among many others. Most divergence events in *Hyospathe*, an Andean-centered genus, and the Andean *Prestoea* clade occurred in the last seven million years, a period

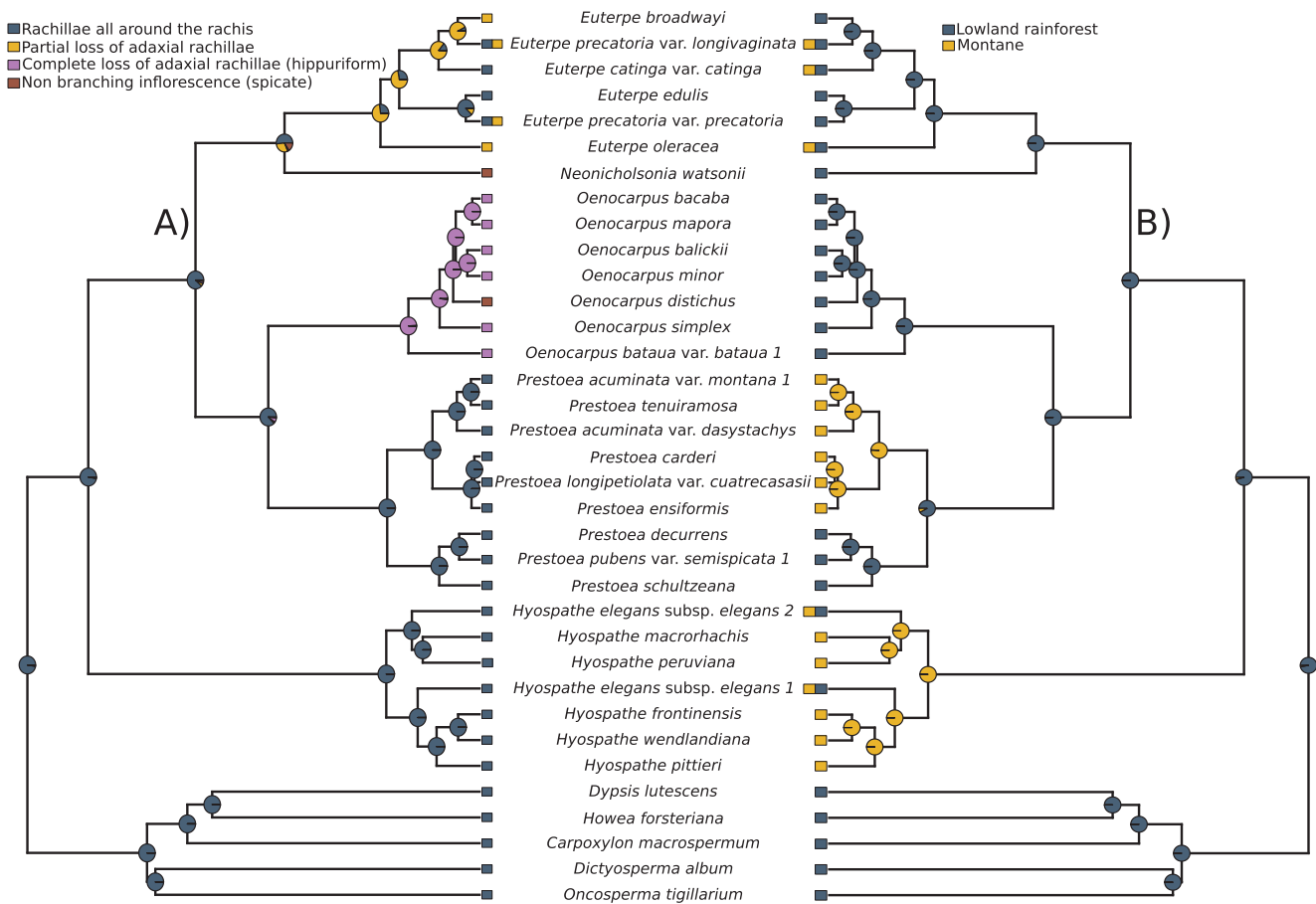


Fig. 5. Ancestral-state reconstruction of A. inflorescence type and B. biome on the Bayesian maximum clade credibility tree of tribe Euterpeae using rayDISC in R. Pie charts show the probability of each state at ancestral nodes.

characterized by an accelerated uplift of the northern Andes (Gregory-Wodzicki, 2000), which could have played a role in the diversification of these lineages.

We estimated that all *Oenocarpus* species had an exclusively Amazonian ancestor, which diversified in the last seven million years. This age postdates estimates of the formation of the transcontinental Amazon River connecting the Atlantic Ocean and the Andes (Hoorn et al., 2017; van Soelen et al., 2017). We conclude that Amazonian *Oenocarpus* species evolved after Lake Pebas had receded (Wesselingh et al., 2002), and the Amazon river had already achieved its current easterly flow. Colonization of the Caribbean occurred twice from South America at ca. 2 Mya, a time when all the Greater and Lesser Antilles were already above water in their current geographic position (Iturralde-Vinent and MacPhee, 1999; Robertson, 2009). Lastly, based on the ancestral range estimation, we propose that the dry forest belt barrier imposed by the Cerrado and Caatinga biomes could have promoted a vicariant split of *Euterpe edulis* from its widespread ancestor in South America by isolating it in the Atlantic forest ca. 1.4 Mya.

4.3. Inflorescence evolution and biome shifts

Our result is concordant with Balick's hypothesis on the evolution of *Oenocarpus*' horse-tail inflorescence from an inflorescence with rachillae all around the main axis, the most common inflorescence type in the tribe. The partial loss of adaxial rachillae occurred at least one time within Euterpeae. However, the total number of shifts could not be determined because two species with partial loss of adaxial rachillae were not sampled (*E. luminosa* A.J.Hend., Galeano & Meza, *E. longibracteata* Barb. Rodr.). Pollinators have been suggested to play an important role on the morphological evolution of inflorescences in

palms (Henderson, 2002). Palm inflorescences have been classified as condensed or elongated based on the length of the peduncle and rachis, and on the branching order of the rachillae (Henderson, 2002). Condensed forms, like in *Oenocarpus*, are more likely to be pollinated by coleopterans, while elongate forms, like in *Prestoea*, are more likely to be pollinated by hymenopterans and dipterans (Henderson, 2002). The evolutionary advantage of condensed inflorescences for coleopteran pollination remains unknown. However, coleopterans have a symbiotic relationship with the palm they pollinate, i.e., the inflorescence temperature is increased during anthesis speeding up egg development and larval growth of flower-breeding pollinators (Ervik and Barfod, 1999; Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al., 2015). This specialized pollination system, however, cannot explain the complete or partial loss of adaxial rachillae. A hypothesis for the loss of adaxial rachillae and pendulous shape of *Oenocarpus* inflorescence is that it evolved in response to the size and amount of fruit it bears. Balick (1986) suggested that this morphology can hold a larger fruit weight (15–20 kg), otherwise the adaxial rachillae would need to be stiffer.

We found two main biome shifts from lowland rainforests to the mountains and other minor shifts by individual taxa within *Euterpe* that have expanded their range to the highlands. This kind of low to high elevation colonization event has been proposed for other taxonomic groups (e.g., Barkman and Simpson, 2001; Brumfield and Edwards, 2007; Chomicki and Renner, 2017; Pérez-Escobar et al., 2017). Our results are concordant with the key role of lowland rainforest taxa as colonizers of montane biomes. Furthermore, our findings agree with the observation that the Andes very rarely constitute the primary source of dispersal into Amazonia (Santos et al., 2009) since only *Hyospathe elegans* expanded its range from the highlands to the lowlands. Previous

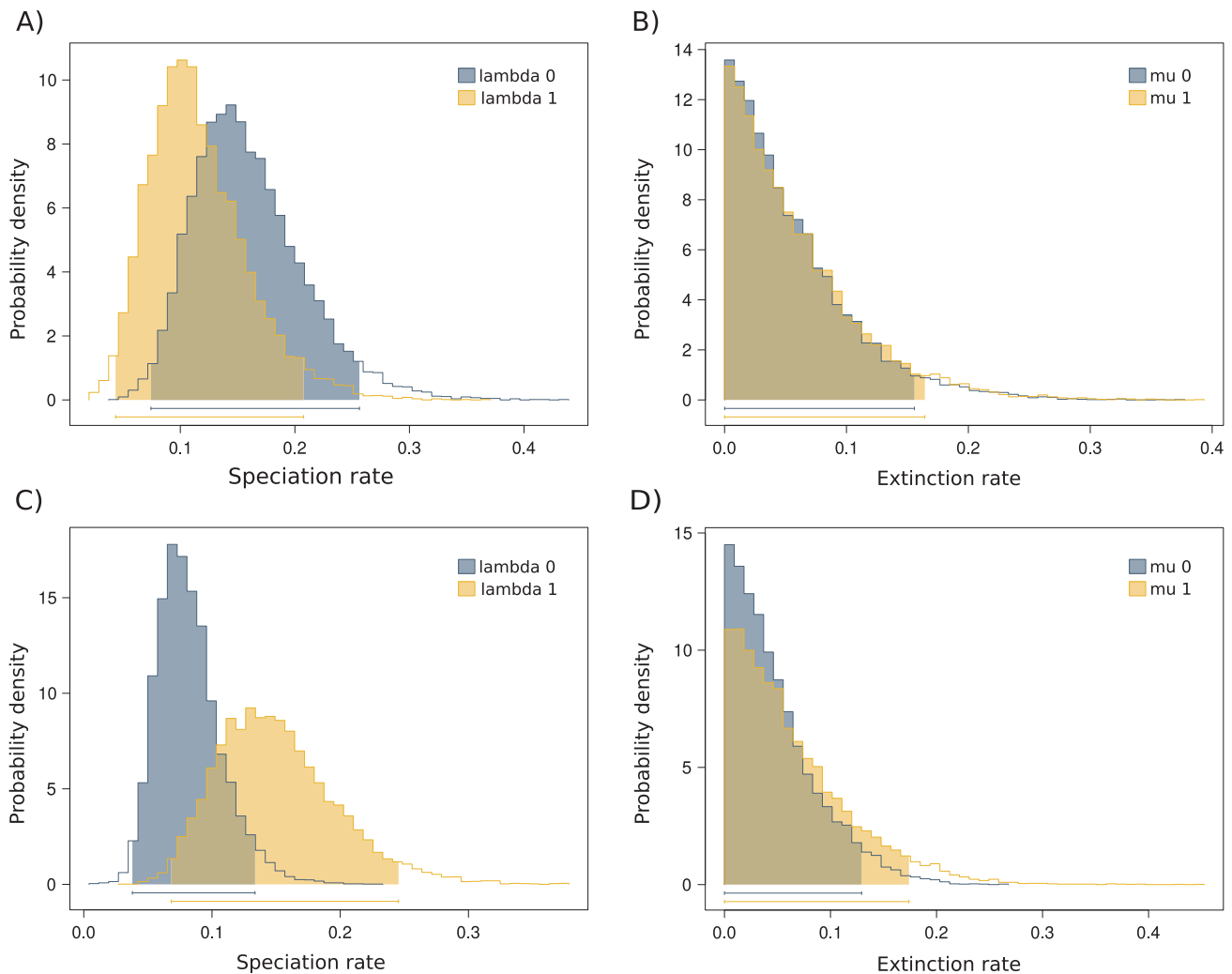


Fig. 6. Result of the Binary State Speciation and Extinction (BiSSE) analysis. A–B: Inflorescence type (0-non-hippuriform, 1-hippuriform). C–D: Biome (0-lowland rainforest, 1-montane). Posterior probability distributions of **A, C** speciation (λ_0 and λ_1) and **B, D** extinction (μ_0 and μ_1).

studies, however, have shown that mountain flora is derived primarily from immigration of cool pre-adapted lineages and that contributions from lowland-adapted lineages are less common (Hughes and Eastwood, 2006; Merckx et al., 2015; Uribe-Convers and Tank, 2015).

4.4. Different diversification rates are associated with biomes but not with inflorescence type

Our study supports Gentry's (1982) hypothesis that Andean-centered taxa are the product of recent and very dynamic speciation, an idea based on floristics and not on actual diversification rates analyses. Several studies on Andean-centered plant taxa have demonstrated increased diversification rates contemporaneous to the Andean orogenic uplift (e.g., Hughes and Eastwood, 2006; Madriñán et al., 2013; Lagomarsino et al., 2016; Pérez-Escobar et al., 2017). These studies proposed that the final period of Andean uplift triggered speciation through the creation of novel niches, or allopatric speciation through isolation. In agreement with these studies, but contrary to our expectations, we found a correlation between montane taxa and increased speciation rates, likely facilitated by the acquisition of new montane adaptations since palms are pre-adapted to lowland rainforest environments (Couvreur et al., 2011).

The coleopteran-*Oenocarpus* relationship was not associated with increased diversification in the Euterpeae. Thus, the coleopteran specialized pollination could not be regarded as a key innovation (sensu

Heard and Hauser, 1995), and our expectation was not met. Flower shape and scent might be more important than inflorescence shape for the specialized beetle pollination (Luis Núñez-Avellaneda pers. comm), and therefore a direct test of the effect of pollinators on palm diversification rates is needed. To accomplish this, more field studies are necessary to identify the exact pollinator guild for each species since currently this information is only available for very few Neotropical palms.

5. Conclusions and perspectives

The first robust dated molecular phylogenetic tree for the economically and ecologically important Neotropical palm tribe Euterpeae is presented here. This phylogenetic tree permitted the reconstruction of the biogeographical history of the tribe and addresses questions on trait-dependent diversification rates.

A complete resolution of all intergeneric relationships allowed addressing the controversy on the taxonomic circumscription of *Jessenia*, *Prestoea* and *Euterpe*. Some interspecific relationships, however, were not resolved and three hyperdominant Neotropical species were non-monophyletic, suggesting that future studies should include several individuals per species and use a high-throughput next generation sequencing approach to fully resolve the phylogeny at the species-level. Gene flow should also be included in future species delimitation and phylogenetic analyses since palms are known to hybridize. Despite

uncertainty in some ancestral area reconstructions, four colonization events from Central to South America were elucidated. Most Euterpeae species diverged in the last 10 million years, and colonized the Caribbean ca. 2 mya.

Tribe Euterpeae's ancestral biome was the lowland rainforest attesting to the importance of lowland adapted lineages on the assembly of montane flora. The two-fold higher speciation rate for montane taxa was contemporaneous to the Andean orogenic uplift and likely facilitated by the acquisition of montane adaptations, which remain to be elucidated. The similar diversification rates among inflorescence types questions the evolutionary importance of the hippuriform inflorescence for beetle-specialized pollination systems.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympcv.2018.12.030>.

Reference

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19, 716–723. <https://doi.org/10.1109/TAC.1974.1100705>.
- Anonymous, 2009. Perfiles de producto: Perfil del palmito. Centro de Información e Inteligencia Comercial (CICO), Ecuador.
- 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. *Proc. Natl. Acad. Sci. U.S.A.* 115, 6034–6039. <https://doi.org/10.1073/pnas.1713819115>.
- Bacon, C.D., Feltus, F.A., Paterson, A.H., Bailey, C.D., 2008. Novel nuclear intron-spanning primers for Arecaceae evolutionary biology. *Mol. Ecol. Resour.* 8, 211–214. <https://doi.org/10.1111/j.1471-8286.2007.01928.x>.
- Bacon, C.D., Velásquez-Fuentes, F.J., Hoorn, C., Antonelli, A., 2018. Iriarteae palms tracked the uplift of Andean Cordilleras. *J. Biogeogr.* 45, 1653–1663. <https://doi.org/10.1111/jbi.13350>.
- 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. *J. Biogeogr.* 40, 274–285. <https://doi.org/10.1111/j.1365-2699.2012.02795.x>.
- Baker, W.J., Savolainen, V., Asmussen-Lange, C.B., Chase, M.W., Dransfield, J., 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. *Syst. Biol.* 58, 240–256. <https://doi.org/10.1093/sysbio/syp021>.
- Balick, M.J., 1986. Systematics and economic botany of the *Oenocarpus-Jessenia* Palmae complex. *Adv. Econ. Bot.* 3, 1–140.
- Barkman, T., Simpson, B., 2001. Origin of high-elevation *Dendrochilum* species (Orchidaceae) endemic to Mount Kinabalu, Sabah Malaysia. *Syst. Bot.* 26, 658–669. <https://www.jstor.org/stable/3093987>.
- Beaulieu, J.M., Oliver, J.C., O'Meara, B.C., 2015. corHMM. R package (Accessed June 2018). < <https://cran.r-project.org/web/packages/corHMM/corHMM.pdf> > .
- Bernal, R., Galeano, G., Henderson, A., 1991. Notes on *Oenocarpus* (Palmae) in the Colombian Amazon. *Brittonia* 43, 154–164. <https://doi.org/10.2307/2807045>.
- Berry, E.W., 1914. The upper Cretaceous and Eocene floras of South Carolina and Georgia (Professional Paper No. 84). Department of the Interior United States Geological Survey.
- Blach-Overgaard, A., Kissling, W.D., Dransfield, J., Balslev, H., Svenning, J.C., 2013. Multimillion-year climatic effects on palm species diversity in Africa. *Ecology* 94, 2426–2435. <https://doi.org/10.1890/12-1577.1>.
- Borchsenius, F., Borgtoft Pedersen, H., Balslev, H., 1998. Manual to the Palms of Ecuador, AAU Reports 37. Aarhus University Press, Denmark.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* 10, e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>.
- Brokamp, G., Valderrama, N., Mittelbach, M., Grandez R., César A., Barfod, Anders S., Weigend, M., 2011. Trade in palm products in north-western south America. *Bot. Rev.* 77, 571–606.
- Brumfield, R.T., Edwards, S.V., 2007. Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnopilus* antshrikes. *Evolution* 61, 346–367. <https://doi.org/10.1111/j.1558-5646.2007.00039.x>.
- Burret, M., 1928. Die palmengattungen *Oenocarpus* Mart. und *Jessenia* Karst., nebst bemerkungen zu *Archontophoenix* H.Wendl. et Drude (einschließlich Loroma O.F. Cook). *Notizblatt des Königl. Botanischen Gartens Museums Berlin* 10, 291–312. <https://doi.org/10.2307/3994678>.
- Burret, M., 1929. Die Gattung *Euterpe* Gaertn. *Bot. Jahrb. Syst.* 63, 49–76.
- Chomicki, G., Renner, S.S., 2017. Partner abundance controls mutualism stability and the pace of morphological change over geologic time. *Proc. Natl. Acad. Sci. U.S.A.* 114, 3951–3956. <https://doi.org/10.1073/pnas.1616837114>.
- 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). *Mol. Phylogenet. Evol.* 97, 32–42.
- 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 Biol.* 9, 44. <https://doi.org/10.1186/1741-7007-9-44>.
- Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458, 754–756. <https://doi.org/10.1038/nature07764>.
- 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. *Mol. Phylogenet. Evol.* 46, 760–775. <https://doi.org/10.1016/j.ympcv.2007.10.010>.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. 772 772. *Nat. Methods* 9. <https://doi.org/10.1038/nmeth.2109>.
- Demesure, B., Sodji, N., Petit, R.J., 1995. A set of universal primers for amplification of polymorphic non-coding regions of mitochondrial and chloroplast DNA in plants. *Mol. Ecol.* 4, 129–134. <https://doi.org/10.1111/j.1365-294X.1995.tb00201.x>.
- Dransfield, J., Uhl, N.W., Asmussen, C.B., Baker, W.J., Harley, M.M., Lewis, C.E., 2008. Genera Palmarum: The Evolution and Classification of Palms. The Board of Trustees of Royal Botanic Gardens, Kew.
- Ervik, F., Feil, J., 1997. Reproductive biology of the monoecious understory palm *Prestoea schultzeana* in Amazonian Ecuador. *Biotropica* 29, 309–317. <https://www.jstor.org/stable/2389146>.
- Ervik, F., Barfod, A., 1999. Thermogenesis in palm inflorescences and its ecological significance. *Acta Bot. Venez.* 22, 195–212. <https://www.jstor.org/stable/44652977>.
- Eiserhardt, W.L., Couvreur, T.L.P., Baker, W.J., 2017. Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytol.* 214, 1408–1422. <https://doi.org/10.1111/nph.14516>.
- Faurby, S., Eiserhardt, W.L., Baker, W.J., Svenning, J.-C., 2016. An all-evidence species-level supertree for the palms (Arecaceae). *Mol. Phylogenet. Evol.* 100, 57–69. <https://doi.org/10.1016/j.ympcv.2016.03.002>.
- FitzJohn, R.G., 2012. Diversitree: comparative phylogenetic analyses of diversification in R. *Meth. Ecol. Evol.* 3, 1084–1092. <https://doi.org/10.1111/j.2041-210X.2012.00234.x>.
- FitzJohn, R.G., Maddison, W.P., Otto, S.P., 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* 58, 595–611. <https://doi.org/10.1093/sysbio/syp067>.
- Futey, M.K., Gandolfo, M.A., Zamalao, M.C., Cúneo, R., Cladera, G., 2012. Arecaceae fossil fruits from the Paleocene of Patagonia, Argentina. *Bot. Rev.* 78, 205–234. <https://doi.org/10.1007/s12229-012-9100-9>.
- Galeano, G., Bernal, R., 2010. Palmas de Colombia: Guía de campo, first ed. Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, Bogotá.
- Gentry, A., 1982. Neotropical floristic diversity - phytogeographical connections between central and south America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny. *Ann. Mo. Bot. Gard.* 69, 557–593. <https://www.jstor.org/stable/2399084>.
- Givnish, T.J., Barfuss, M.H.J., Van Ee, B., Riina, R., Schulte, K., Horres, R., Gonsiska, P.A., Jabaily, R.S., Crayn, D.M., Smith, J.A.C., et al., 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Mol. Phylogenet. Evol.* 71, 55–78. <https://doi.org/10.1016/j.ympcv.2013.10.010>.
- Gregory-Wodzicki, K., 2000. Uplift history of the central and northern Andes: a review. *Geol. Soc. Am. Bull.* 112, 1091–1105. [https://doi.org/10.1130/0016-7606\(2000\)112<1091:UHOTCA>2.0.CO;2](https://doi.org/10.1130/0016-7606(2000)112<1091:UHOTCA>2.0.CO;2).
- Harley, M.M., 2006. A summary of fossil records for Arecaceae. *Bot. J. Linn. Soc.* 151, 39–67. <https://doi.org/10.1111/j.1095-8339.2006.00522.x>.
- Heard, S.B., Hauser, D.L., 1995. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.* 10, 151–173. <https://doi.org/10.1080/10292389509380518>.
- Henderson, A.J., 1999. A phylogenetic analysis of the Euterpeinae (Palmae; Arecaceae; Arecaceae) based on morphology and anatomy. *Brittonia* 51, 106–113. <https://doi.org/10.2307/2666565>.
- Henderson, A., 2002. Evolution and Ecology of Palms. New York Botanical Garden Press, New York.
- Henderson, A.J., 2004. A multivariate analysis of *Hyospathe* (Palmae). *Am. J. Bot.* 91, 953–965. <https://doi.org/10.3732/ajb.91.6.953>.

- Henderson, A.J., Galeano, G., 1996. *Euterpe, Prestoea, and Neonicholsonia* (Palmae). *Flora Neotrop.* 72, 1–89. <https://www.jstor.org/stable/4393873>.
- Henderson, A.J., Galeano, G., Bernal, R., 1995. *Field guide to the palms of the Americas*. Princeton University Press, Princeton, New Jersey.
- Ho, S.Y.W., Phillips, M.J., 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Syst. Biol.* 58, 367–380. <https://doi.org/10.1093/sysbio/syp035>.
- Hollick, A., 1928. Paleobotany of Porto Rico, in: *Scientific survey of Porto Rico and Virgin Islands*, vol. 7, pt. 3. New York Academy of Science, New York, pp. 177–393.
- Hoorn, C., 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 105, 267–309. [https://doi.org/10.1016/0031-0182\(93\)90087-Y](https://doi.org/10.1016/0031-0182(93)90087-Y).
- Hoorn, C., 1994. Fluvial palaeoenvironments in the intracratonic Amazonas basin (early Miocene—early middle Miocene, Colombia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109, 1–54. [https://doi.org/10.1016/0031-0182\(94\)90117-1](https://doi.org/10.1016/0031-0182(94)90117-1).
- Hoorn, C., Bogotá-A. G.R., Romero-Baez, M., Lammertsma, E.I., Flantua, S.G.A., Hoorn, C., Bogotá-A. G.R., Romero-Baez, M., Lammertsma, E.I., Flantua, S.G.A., Dantas, E.L., Dino, R., do Carmo, D.A., Chemale Jr, F., 2017. The Amazon at sea: onset and stages of the Amazon river from a marine record, with special reference to Neogene plant turnover in the drainage basin. *Global Planet. Change* 153, 51–65.
- Hughes, C., Eastwood, R., 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci. U.S.A.* 103, 10334–10339. <https://doi.org/10.1073/pnas.0601928103>.
- Iturralde-Vinent, M., MacPhee, R.D.E., 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* 238, 1–95. <http://hdl.handle.net/2246/1642>.
- Jenkins, C.N., Pimm, S.L., Joppa, L.N., 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci. U.S.A.* 110, E2602–E2610. <https://doi.org/10.1073/pnas.1302251110>.
- Kang, J., Thakali, K.M., Xie, C., Kondo, M., Tong, Y., Ou, B., Jensen, G., Medina, M.B., Schauss, A.G., Wu, X., 2012. Bioactivities of açai (*Euterpe precatoria* mart.) fruit pulp, superior antioxidant and anti-inflammatory properties to *Euterpe oleracea* Mart. *Food Chem.* 133, 671–677. <https://doi.org/10.1016/j.foodchem.2012.01.048>.
- Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. <https://doi.org/10.1093/molbev/mst010>.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., Drummond, A., 2012. Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28, 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>.
- Koenen, E.J.M., de Vos, J.M., Atchison, G.W., Simon, M.F., Schrire, B.D., de Souza, E.R., de Queiroz, L.P., Hughes, C.E., 2013. Exploring the tempo of species diversification in legumes. *S. Afr. J. Bot.* 89, 19–30. <https://doi.org/10.1016/j.sajb.2013.07.005>.
- Küchmeister, H., Silberbauer-Gottsberger, I., Gottsberger, G., 1997. Flowering, pollination, nectar standing crop, and nectaries of *Euterpe precatoria* (Arecaceae), an Amazonian rain forest palm. *Plant Syst. Evol.* 206, 71–97. <https://doi.org/10.1007/BF00987942>.
- Lagomarsino, L.P., Condamine, F.L., Antonelli, A., Mulch, A., Davis, C.C., 2016. The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytol.* 210, 1430–1442. <https://doi.org/10.1111/nph.13920>.
- Listabarth, C., 2001. Palm pollination by bees, beetles and flies: Why pollinator taxonomy does not matter. The case of *Hyospathe elegans* (Arecaceae, Arecoideae, Arecaceae, Euterpeinae). *Plant Spec. Biol.* 16, 165–181. <https://doi.org/10.1046/j.1442-1984.2001.00061.x>.
- Lorenzi, H., Noblick, L.R., Kahn, F., Ferreira, E., 2010. *Brazilian Flora: Arecaceae*. Instituto Plantarum de estudos da flora Ltda., Brazil.
- Ludeña, B., Chabrilange, N., Aberlenc-Bertossi, F., Adam, H., Tregear, J.W., Pintaud, J.C., 2011. Phylogenetic utility of the nuclear genes AGAMOUS 1 and PHYTOCHROME B in palms (Arecaceae): an example within Baccharidaceae. *Ann. Bot.* 108, 1433–1444. <https://doi.org/10.1093/aob/mcr191>.
- Maddison, W.P., FitzJohn, R.G., 2015. The unsolved challenge to phylogenetic correlation tests for categorical characters. *Syst. Biol.* 64, 127–136. <https://doi.org/10.1093/sysbio/syu070>.
- Maddison, W.P., Midford, P.E., Otto, S.P., Oakley, T., 2007. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56, 701–710. <https://doi.org/10.1080/10635150701607033>.
- Madriñán, S., Cortés, A.J., Richardson, J.E., 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Front. Genet.* 4, 192. <https://doi.org/10.3389/fgene.2013.00192>.
- Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Front. Biogeogr.* 5, 242–248. <https://scholarship.org/uc/item/44j7n141>.
- Meerow, A.W., Noblick, L., Borrone, J.W., Couvreur, T.L.P., Mauro-Herrera, M., Hahn, W.J., Kuhn, D.N., Nakamura, K., Oleas, N.H., Schnell, R.J., 2009. Phylogenetic analysis of seven WRKY genes across the palm subtribe Attaleinae (Arecaceae) identifies *Syagrus* as sister group of the coconut. *PLoS One* 4, e7353. <https://doi.org/10.1371/journal.pone.0007353>.
- Merckx, V.S.F.T., Hendriks, K.P., Beentjes, K.K., Mennes, C.B., Becking, L.E., Peijnenburg, K.T.C.A., Afendy, A., Arumugam, N., de Boer, H., Biun, A., et al., 2015. Evolution of endemism on a young tropical mountain. *Nature* 524, 347–350. <https://doi.org/10.1038/nature14949>.
- Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, November 2010, New Orleans, pp. 1–8. < <https://xplore.staging.ieee.org/servlet/opac?punumber=5668967> > .
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodríguez-Parra, L.A., Ramirez, V., Niño, H., 2015. Middle Miocene closure of the central American seaway. *Science* 348, 226–229.
- Montúfar, R., Pintaud, J.C., 2008. Estatus taxonómico de *Oenocarpus bataua* (Euterpeae, Arecaceae) inferido por secuencias del ADN cloroplástico. *Rev. Peru. Biol.* 15, 73–78. <https://doi.org/10.15381/rpb.v15i3.2988>.
- Montúfar, R., Laffargue, A., Pintaud, J.-C., Hamon, S., Avallone, S., Dussert, S., 2010. *Oenocarpus bataua* Mart. (Arecaceae): rediscovering a source of high oleic vegetable oil from Amazonia. *J. Am. Oil Chem. Soc.* 87, 167–172. <https://doi.org/10.1007/s11746-009-1490-4>.
- Nieto-Blázquez, M.E., Antonelli, A., Roncal, J., 2017. Historical biogeography of endemic seed plant genera in the Caribbean: Did GAARlandia play a role? *Ecol. Evol.* 7, 10158–10174. <https://doi.org/10.1002/ece3.3521>.
- Núñez-Avellaneda, L.A., Rojas-Robles, R., 2008. Reproductive biology and pollination ecology of the milpesos palm *Oenocarpus bataua* on the Colombian Andes. *Caldasia* 30, 101–125.
- Núñez-Avellaneda, L.A., Isaza, C., Galeano, G., 2015. Ecología de la polinización de tres especies de *Oenocarpus* (Arecaceae) simpátricas en la Amazonia Colombiana. *Rev. Biol. Trop.* 63, 35–55. <https://doi.org/10.15517/rbt.v63i1.13030>.
- Odendaal, A.Y., Schauss, A.G., 2014. Potent antioxidant and anti-inflammatory flavonoids in the nutrient-rich Amazonian palm fruit, açai (*Euterpe* spp.). In: Watson, R.R., Preedy, V.R., Zibadi, S. (Eds.), *Polyphenols in Human Health and Disease*. Academic Press, San Diego, pp. 219–239.
- Olson, D., Dinerstein, E., Wikramanayake, E., Burgess, N., Powell, G., Underwood, E., D'Amico, J., Itoua, I., Strand, H., Morrison, J., et al., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2).
- Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis, R.B., Joyce, W.G., Ksepka, D.T., Patane, J.S.L., Smith, N.D., Tarver, J.E., van Tuinen, M., Yang, Z., Angielczyk, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Muller, J., Smith, K.T., Theodor, J.M., Warnock, R.C.M., Benton, M.J., 2012. Best practices for justifying fossil calibrations. *Syst. Biol.* 61, 346–359. <https://doi.org/10.1093/sysbio/syr107>.
- Pérez-Escobar, O.A., Chomicki, G., Condamine, F.L., Karremans, A.P., Bogarin, D., Matzke, N.J., Silvestro, D., Antonelli, A., 2017. Recent origin and rapid speciation of Neotropical orchids in the world's richest plant biodiversity hotspot. *New Phytol.* 215, 891–905. <https://doi.org/10.1111/nph.14629>.
- Poinar, G.J., 2002. Fossil palm flowers in Dominican and Mexican amber. *Bot. J. Linn. Soc.* 138, 57–61. <https://doi.org/10.1046/j.1095-8339.2002.00010.x>.
- Pyhälä, A., Brown, K., Adger, W.N., 2006. Implications of livelihood dependence on non-timber products in Peruvian Amazonia. *Ecosystems* 9, 1328–1341. <https://doi.org/10.1007/s10021-005-0154-y>.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* 67, 901–904. <https://doi.org/10.1093/sysbio/syy032>.
- Robertson, R.E.A., 2009. *Antilles, Geology*. In: Gillispie, R.G., Clague, D.A. (Eds.), *Encyclopedia of Islands*. University of California Press, pp. 29–35.
- Roncal, J., Francisco-Ortega, J., Asmussen, C.B., Lewis, C.E., 2005. Molecular phylogenetics of tribe Geonomeae (Arecaceae) using nuclear DNA sequences of Phosphoribulokinase and RNA Polymerase II. *Syst. Bot.* 30, 275–283. <https://doi.org/10.1600/0363644054223620>.
- Roncal, J., Borchsenius, F., Lange, C.B.A., Balslev, H., 2010. Divergence times in the tribe Geonomeae (Arecaceae) coincide with Tertiary geological events. In: Seberg, O., Petersen, G., Barfod, A.S., Davis, J.I. (Eds.), *Diversity, Phylogeny, and Evolution in the Monocotyledons*. Aarhus University Press, Aarhus, pp. 245–265.
- Salamanca Villegas, S., van Soelen, E.E., Teunissen van Manen, M.L., Flantua, S.G.A., Santos, R.V., Roddaz, M., Dantas, E.L., van Loon, E., Sinninghe Damsté, J.S., Kim, J.-H., Hoorn, C., 2016. Amazon forest dynamics under changing abiotic conditions in the early Miocene (Colombian Amazonia). *J. Biogeogr.* 43, 2424–2437. <https://doi.org/10.1111/jbi.12769>.
- Sanín, M.J., Kissling, W.D., Bacon, C.D., Borchsenius, F., Galeano, G., Svenning, J.-C., Olivera, J., Ramírez, R., Trénel, P., Pintaud, J.-C., 2016. The Neogene rise of the tropical Andes facilitated diversification of wax-palms (*Ceroxylon*: Arecaceae) through geographical colonization and climatic niche separation. *Bot. J. Linn. Soc.* 182, 303–317. <https://doi.org/10.1111/boj.12419>.
- Santos, J.C., Coloma, L.A., Summers, K., Caldwell, J.P., Ree, R., Cannatella, D.C., 2009. Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biol.* 7, 448–461. <https://doi.org/10.1371/journal.pbio.1000056>.
- Saxena, R.K., Khare, S., Misra, N.K., 1992. *Echimonoporopolis*, a new pollen genus from the Nevelly formation of Jayamkondacholapuram well-12, Tiruchirappalli District, Tamil Nadu. *Palaeobotanist* 39, 46–49.
- Schultz, E.D., Burney, C.W., Brumfield, R.T., Polo, E.M., Cracraft, J., Ribas, C.C., 2017. Systematics and biogeography of the automolus infuscatum complex (aves; furnariidae): Cryptic diversity reveals western amazonia as the origin of a transcontinental radiation. *Mol. Phylogenet. Evol.* 107, 503–515. <https://doi.org/10.1016/j.ympev.2016.12.023>.
- Serrano-Serrano, M.L., Rolland, J., Clark, J.L., Salamin, N., Perret, M., 2017. Hummingbird pollination and the diversification of angiosperms: an old and successful association in Gesneriaceae. *Proc. R. Soc. B-Biol. Sci.* 284, 20162816. <https://doi.org/10.1098/rspb.2016.2816>.
- Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T., Hughes, C.E., 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci. U.S.A.* 106, 20359–20364. <https://doi.org/10.1073/pnas.0903410106>.

- Skov, F., Balslev, H., 1989. A revision of *Hyospathe* (Arecaceae). *Nord. J. Bot.* 9, 189–202. <https://doi.org/10.1111/j.1756-1051.1989.tb02114.x>.
- Stamatakis, A., 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C.V., Magnusson, W.E., Molino, J.-F., Monteagudo, A., Núñez Vargas, P., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.-H., Guimarães Vieira, I.C., Amaral, I.L., Brien, R., Castellanos, H., Cárdenas López, D., Duivenvoorden, J. F., Mogollón, H.F., Matos, F.D. de A., Dávila, N., García-Villacorta, R., Stevenson Diaz, P.R., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Fernandez Piedade, M.T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard, C. G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D. de A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Cornejo Valverde, F., Di Fiore, A., Jimenez, E.M., Peñuela Mora, M.C., Phillips, J.F., Rivas, G., van Andel, T.R., von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Trindade Nascimento, M., Ramirez-Angulo, H., Sierra, R., Tirado, M., Umaña Medina, M.N., van der Heijden, G., Vela, C.I.A., Vilanova Torre, E., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Urrego Giraldo, L.E., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Palacios Cuenca, W., Pauletto, D., Valderrama Sandoval, E., Valenzuela Gamarra, L., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G., Silman, M.R., 2013. Hyperdominance in the Amazonian tree flora. *Science* 342, 1243092–1243092. < <https://doi.org/10.1126/science.1243092> > .
- The Nature Conservancy, 2009. Terrestrial Ecoregions of the World (Accessed November 2017). < <http://maps.tnc.org/files/metadata/TerrEcos.xml> > .
- Tripp, E.A., Tsai, Y.E., 2017. Disentangling geographical, biotic, and abiotic drivers of plant diversity in Neotropical *Ruellia* (Acanthaceae). *PLoS One* 12, e0176021. <https://doi.org/10.1371/journal.pone.0176021>.
- Uribe-Convers, S., Tank, D.C., 2015. Shifts in diversification rates linked to biogeographic movement into new areas: an example of a recent radiation in the Andes. *Am. J. Bot.* 102, 1854–1869. <https://doi.org/10.3732/ajb.1500229>.
- van Soelen, E.E., Kim, J.H., Santos, R.V., Dantas, E.L., Vasconcelos de Almeida, F., Pires, J.P., Roddaz, M., Sinnighe Damsté, J.S., 2017. A 30 Ma history of the Amazon River inferred from terrigenous sediments and organic matter on the Ceará Rise. *Earth Planet. Sci. Lett.* 474, 40–48. <https://doi.org/10.1016/j.epsl.2017.06.025>.
- Veranso-Libalah, M.C., Kadereit, G., Stone, R.D., Couvreur, T.L.P., 2018. Multiple shifts to open habitats in Melastomataceae (Melastomataceae) congruent with the increase of African Neogene climatic aridity. *J. Biogeogr.* 45, 1420–1431. <https://doi.org/10.1111/jbi.13210>.
- Wesselingh, F.P., Räsänen, M.E., Irion, G., Vonhof, H.B., Kaandorp, R., Renema, W., Romero Pittman, L., Gingras, M., 2002. Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainozoic Res.* 1, 35–68.
- Wessels Boer, J., 1965. *The Indigenous Palms of Suriname*. E.J. Brill, Leiden.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* 13, 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>.