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Cenozoic colonization and diversification patterns of tropical American palms: evidence from *Astrocaryum* (Arecaceae)

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With 788 species in 67 genera in the Neotropics, Arecaceae are an important ecological and economic component of the region. We review the influence of geological events such as the Pebas system, the Andean uplift and the land connections between South and Central/North America, on the historical assembly of Neotropical palms. We present a case study of the palm genus *Astrocaryum* (40 species) as a model for evaluating colonization and diversification patterns of lowland Neotropical taxa. We conducted a Bayesian dated phylogenetic analysis based on four low-copy nuclear DNA regions and a biogeographical analysis using the dispersal, extinction and cladogenesis model. Cladogenesis of Western Amazonian *Astrocaryum* spp. (*c*. 6 Mya) post-dated the drainage of the aquatic Pebas system, supporting the constraining role of Pebas on *in situ* diversification and colonization. The ancestral distribution of *Astrocaryum* spp. in the Guiana Shield supported the hypothesis of an old formation that acted as a source area from which species colonized adjacent regions, but an earliest branching position for Guianan species was not confidently recovered. A twofold increase in diversification rate was found in a clade, the ancestor of which occupied the Guiana Shield (*c*. 13 Mya, a time of climatic change and Andean uplift). © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **171**, 120–139.

ADDITIONAL KEYWORDS: ancestral range reconstruction – Andean uplift – dispersal, extinction and cladogenesis (DEC) model – diversification rate shifts – Guiana Shield – middle Miocene climatic optimum – Pebas – Western Amazon.

INTRODUCTION

DIVERSITY AND EVOLUTIONARY HISTORY OF NEOTROPICAL PALMS

Palms (Arecaceae) grow in a diversity of habitats in the Neotropics, including flooded and unflooded lowland forests, montane forests and savannahs, reaching their highest diversity and abundance in Western Amazonia (Kahn & de Granville, 1992; Dransfield *et al*., 2008). For example, one study of a terra firme unflooded forest of the lower Ucayali River valley in Peru documented 7000 palm individuals in 29 species in a 0.71-ha plot (Kahn & de Granville, 1992). Palms are important components of forest structure and dynamics, occupying different strata in the understory and canopy and providing habitat and food for animals (e.g. Kahn & de Granville, 1992). The economic importance of palms as a source of construction material, fibre, food, medicine and ornamentals is rapidly evident on a visit to rural communities in the Tropics (e.g. Sosnowska & Balslev, 2009). Species diversity in the palm family in the Neotropics consists of 788 species in 67 genera, representing four of the five subfamilies recognized. However, most species diversity is concentrated in Arecoideae, the most species-rich subfamily of palms (Baker *et al*., 2009). Only the monotypic subfamily Nypoideae is not

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Table 1. Neotropical palm species diversity. Number of species and genera for each Neotropical lineage above the genus level (subtribe or tribe)

Lineage	Number of genera	Number of species
Bactridinae	6	166
Attaleineae	7	150
Chamaedoreeae	4	118
Geonomateae	6	99
Cryosophileae	10	82
Trachycarpeae	7	41
Iriarteeae	5	32
Euterpeae	5	29
Sabaleae	1	16
Ceroxyleae	2	13
Roystoneeae	1	10
Mauritiinae	3	7
Phytelepheae	3	7
Reinhardtieae	1	6
Cyclospatheae	1	4
Elaeidinae	2	3
Leopoldinieae	1	2
Manicarieae	1	2
Rhaphiinae	1	1
Total	67	788

native to the Neotropics, although its distinctive pollen occurs in the fossil record of the Americas, appearing in Central and South America in the Maastrichtian (Gee, 2001). The Arecoideae contain the largest predominantly Neotropical tribes within the palm family, such as Cocoseae (*c.* 319 species) and Chamaedoreeae (*c.* 118 species). Table 1 presents the distribution of Neotropical species and genera across 19 tribes or subtribes of Arecaceae. Most genera are endemic to the Neotropics, except for *Raphia* P.Beauv, *Elaeis* Jacq. (oil palm), and *Cocos* L. *Nypa* Steck is native to the Old World Tropics but has been naturalized in West Africa and the eastern coast of tropical America (Dransfield *et al.*, 2008). Research on the abiotic and biotic determinants of palm species distribution, community composition and species richness has been recently reviewed (Eiserhardt *et al.*, 2011a). Notably, higher water and soil nutrient availability can predict higher palm species richness in the Americas (Bjorholm *et al.*, 2006; Kreft, Sommer & Barthlott, 2006).

Because of their importance in tropical ecosystems, the taxonomy and systematic relationships of palms has been a major research focus since the 19th century. This has yielded a wealth of knowledge on the family (e.g. Dransfield *et al.*, 2008), making Arecaceae one of the most well-known tropical plant families, especially in the Neotropics. Many recent studies have focused on higher level phylogenetic relationships between genera, culminating in the first complete genus phylogenetic tree of the family (Baker *et al.*, 2009). In parallel, numerous studies have provided a better understanding of the evolutionary and biogeographic history of the family (Gunn, 2004; Savolainen *et al.*, 2006; Trénel *et al.*, 2007; Cuenca, Asmussen-Lange & Borchsenius, 2008; Roncal *et al.*, 2010; Couvreur, Forest & Baker, 2011; Eiserhardt *et al.*, 2011b; Bacon, Baker & Simmons, 2012a). In a recent molecular study, palms were shown to have initially diversified in Laurasia during the mid-Cretaceous (Couvreur *et al.*, 2011). Baker & Couvreur (in press, a, b) undertook a detailed analysis of palm biogeography and showed that, from this ancestral area, palms migrated at different time periods into their present day distributions, including South America. When looking at higher-level biogeographic patterns (above the genus level), the analysis identified four major dispersal events into South America, three from North/Central America and one from Africa. The dating of these events remains coarse, but three events occurred during the end of the Cretaceous and early Cenozoic (*c.* 75–55 Mya) and one during the later Palaeogene (*c.* 40–35 Mya). Arecoideae, which are so dominant in the Neotropical palm flora, appear to have colonized South America on a single occasion, dispersing from North/Central America *c.* 75 Mya (Baker & Couvreur, in press, a, b). The other dispersal events account for only a fraction of the diversity: Mauritiinae (seven species), Ceroxyloideae (20 South American species) and Cryosophileae (eight South American species). From South America, there were several back dispersals into Central/North America at higher and lower taxonomic levels (i.e. between and within genera), as well as dispersal events into Palaeotropical regions. The large majority of Neotropical palms have originated *in situ* in South America and, even although they are strictly speaking immigrants (*sensu* Pennington & Dick, 2004), having dispersed from Laurasia millions of years ago, most of this richness appears to be autochthonous (Bjorholm *et al.*, 2006; Baker & Couvreur, in press, a, b).

GEOLOGICAL EVENTS INFLUENCING THE HISTORICAL ASSEMBLY OF NEOTROPICAL PALMS

Biogeographic inferences based on dated phylogenetic trees have provided insights into how past geological and climatic events have influenced the diversification, extinction and migration of Neotropical lineages (Hoorn *et al.*, 2010; Antonelli & Sanmartin, 2011). In palms, there is also growing evidence of the influence of these factors on their evolution. The Andes acted as a geographical barrier to dispersal for lowland plant species, as an area of speciation and as an area to and from which colonization occurred (e.g. Chapman, 1926; Antonelli *et al*., 2009, and references therein; Barfod, Trénel & Borchsenius, 2010; Eiserhardt *et al*., 2011b). Andean upheaval may have triggered the allopatric diversification of lowland palm lineages (Andean uplift vicariance hypothesis; Chapman, 1926). For example, diversification patterns and timing of tribe Phytelepheae (eight species) corresponded to the sequential uplift of the northern Andean cordilleras (Trénel *et al*., 2007; Barfod *et al*., 2010). Similarly, the diversification of extant lineages in *Attalea* Kunth (69 species, crown node at *c*. 13 Mya), and the split of *Jubaea* Kunth (one species) and *Butia* Becc. (nine species) at *c*. 14.5 Mya, also coincided with the formation period of the northern and central Andes (Meerow *et al*., 2009). There is, however, some evidence of trans-Andean dispersal among palm populations of *Oenocarpus bataua* Mart. during the Quaternary (Montúfar, 2007). Andean uplift from the Miocene through the Pliocene may have also triggered *in situ* diversification through the availability of new habitat in *Aiphanes* Willd. (24 species; Eiserhardt *et al*., 2011b), *Ceroxylon* Humb. & Bonpl. (11 species; Trénel *et al*., 2007) and the high-elevation *Geonoma* Willd. clade (five species; Roncal *et al*., 2010; Henderson, 2011). However, increased rates of speciation in these clades relative to lowland lineages have not been tested in these studies. Geographical distribution and phylogenetic position of some of these Andean-centred taxa suggest a secondary dispersal into lowland habitats (as in *Aiphanes horrida* (Jacq.) Burret and *Wettinia augusta* Poepp. & Endl.) or even to the Antilles (as in *Geonoma undata* Klotzsch).

Flooding of Western Amazonia attributable to the uplift of the eastern cordillera of the Central Andes caused the emergence of an aquatic system called Lake Pebas or the Pebas Sea (*c*. 23–8 Mya; Hoorn, 1994; Wesselingh *et al*., 2002; Wesselingh & Salo, 2006), which may have hampered Western Amazonian speciation and plant dispersal between the Andes and Amazonia for at least 6 Myr (Antonelli *et al*., 2009). Controversy exists on whether Pebas was an intra-continental seaway, a fluvial system, a large single lake or a system of wetlands, and the degree of marine influence it received from the Caribbean (Räsänen *et al*., 1995; Lundberg *et al*., 1998; Wesselingh *et al*., 2002; Wesselingh & Salo, 2006; Antonelli *et al*., 2009; Hoorn *et al*., 2010; Latrubesse *et al*., 2010). In Arecaceae, biogeographic reconstructions shedding light on the influence of the Pebas system on species diversification are scarce. Divergence time of the Andean *Parajubaea* Burret (three species) and Bolivian–Brazilian *Allagoptera* Nees (five species) at *c*. 24 Mya coincides with the formation of the Pebas system, leading Meerow *et al*. (2009) to propose that this system could have caused a vicariant event separating a widespread ancestor of *Parajubaea*/*Allagoptera*. *Wendlandiella* Dammer, a monotypic genus native to western Amazonia, split from the rest of the American genera of tribe Chamaedoreeae during the Eocene *c*. 45 Mya (Cuenca *et al*., 2008). Whether *Wendlandiella* diversified in Amazonia with subsequent extinction of most species during the Pebas period, or it did not diversify despite its long occupation in Amazonia, has not been tested.

The closure of the Isthmus of Panama, estimated at *c*. 3 Mya, has been recently challenged by evidence from Farris *et al*. (2011) of an initial fracturing of the isthmus during collision with the South American plate estimated at 23–25 Mya. This finding supports numerous Miocene migrations between North and South America proposed in biogeographic studies of plants and animals (e.g. Bacon *et al*., 2012b, and others some reviewed in Cody *et al*., 2010; Pennington & Dick, 2010). The relative role of the closure of the isthmus in facilitating inter-American biotic interchange also needs reconsideration because of increasing reports of transoceanic dispersals in palms (Gunn, 2004; Bjorholm *et al*., 2006; Trénel *et al*., 2007; Cuenca *et al*., 2008; Meerow *et al*., 2009; Bacon *et al*., 2012a) and other plant families (e.g. Pennington & Dick, 2004). However, geographical distributions of several palms find their northern or southern limits at this continental junction (e.g. *Oenocarpus bataua* and *Mauritia flexuosa* L.f. in South America and species of *Chamaedorea* Willd. in Central America). Dated phylogenetic trees of tropical American palm lineages have revealed a geographical structure with a nested South American clade or a nested Central American clade and migration ages through the Isthmus of Panama earlier than 3 Mya, supporting the hypothesis of Farris *et al*. (2011) of an earlier isthmus formation. An arrival from South to North America of the Neotropical Chamaedoreeae has been proposed to have occurred in the mid-Eocene, probably using the proto-greater Antilles (*c*. 50 Mya; Graham, 2003) migration route (Cuenca *et al*., 2008). Subsequently, at least two independent back dispersal events to South America (by the *Chamaedorea linearis-fragrans* Mart. clade at *c*. 18 Mya, and more recently by *Synechanthus warscewiczianus* H.Wendl.), and one dispersal to the Antilles by *Gaussia* H.Wendl at *c*. 20 Mya, were described (Cuenca *et al*., 2008). In tribe Geonomateae, the ancestor of *Calyptronoma* Griseb./*Calyptrogyne* H.Wendl. (a clade of 21 species distributed in the Greater Antilles and Central America) was hypothesized to colonize the Antilles after 27 Mya (Roncal *et al*., 2010), and thus the Greater Antilles and Aves Ridge (35–33 Mya; Iturralde-Vinent & MacPhee, 1999), probably played no role as a migration route for this lineage. Pliocene dispersal through short water barriers has been suggested in *Pseudophoenix* H.Wendl. (four species) from North/Central America to the Antilles *c.* 4 Mya (Trénel *et al.*, 2007; Baker & Couvreur, in press, a, b).

Although not as diverse as Western Amazonia, the Guiana Shield is also an important centre of biodiversity as it houses approximately 25% of the remaining tropical evergreen forest and approximately 20 000 vascular plant species (Guayana Shield Conservation Priority Setting Workshop, 2002). It has been hypothesized that the marine incursions, the Pebas mega-lake and the Palaeo-Orinoco system provoked an isolation and diversification of species in the old formations of the Guiana and Brazilian Shields, whereas lowland species were prone to extinction (Webb, 1995; Antonelli & Sanmartin, 2011). The Guiana Shield as a relatively stable old formation could thus have harboured the ancestors of many extant plant species that later colonized the drained parts of Amazonia and the rising Andes. However, no evidence exists of Guiana Shield palm species forming a clade sister to the rest of the subfamily, tribe or genus members.

THE CASE OF *ASTROCARYUM*

Astrocaryum G.Mey. is one of the six genera of subtribe Bactridinae in tribe Cocoseae. It comprises 40 species (Kahn, 2008), distributed from Central America to Brazil and Bolivia, mostly found below 1000 m of elevation (except for *A. faranae* F.Kahn & E.Ferreira growing up to 1650 m in Peru). *Astrocaryum* spp. grow in a wide variety of habitats in primary or secondary lowland rainforests, such as riparian and swamp forests, white sand savannahs, terra firme on clayey soils, inter-Andean valleys, semi-arid cerrado vegetation and the Brazilian coastal Atlantic forest (Dransfield *et al.*, 2008; Kahn, 2008). The resurrection of the genus *Hexopetion* Burret as distinct from *Astrocaryum* has been proposed based on anatomical and morphological characters (Pintaud, Millán & Kahn, 2008; Millán & Kahn, 2010) to comprise two species (*H. alatum* (H.F.Loomis) F.Kahn & Pintaud and *H. mexicanum* (Liebm. ex Mart.) Burret) restricted to Central America. However, recognition of this genus is not widely accepted (Dransfield *et al.*, 2008). Recent phylogenetic analyses of the subtribe using nuclear and plastid DNA regions (Ludeña *et al.*, 2011; Eiserhardt *et al.*, 2011b) have provided insight into this controversy. In Eiserhardt *et al.* (2011b), *Hexopetion* was sister to *Astrocaryum*, with 98% maximum likelihood and 94% maximum parsimony bootstrap support values. However, in Ludeña *et al.* (2011), the sister relationship between these two genera was only weakly supported by a maximum likelihood bootstrap of 41%. *Astrocaryum* has been subject to numerous ecological studies such as population dynamics and dispersal (e.g. Cintra & Horna, 1997; Galetti *et al.*, 2006), reproductive biology (e.g. Consiglio & Bourne, 2001), conservation and ethnobotany (e.g. Coomes, 2004). Several species are widely used by Amerindian communities as source of oil, fibre and food (Kahn, 2008).

To achieve a comprehensive understanding of the historical assembly of the high species diversity in the Neotropics, studies across multiple plant and animal groups and different timescales are needed. We used the palm genus *Astrocaryum* as a model to study the biogeographic history of the Neotropics, because it can provide insight into the evolution of lowland Amazonian-centred genera (as opposed to Andean-centred genera; Gentry, 1982). Our objectives were to detect patterns of migration and diversification among and within different tropical American regions, and to test whether shifts in diversification rates can be associated with specific geological or climatic events. We specifically asked: (1) did the Pebas system represent a barrier of colonization to Western Amazonia and can we provide some insight on the widespread lake vs. fluvial system hypotheses of Pebas?; (2) did the Guiana Shield represent a source from which species colonized other adjacent areas in tropical America, i.e. are *Astrocaryum* spp. of this area sister to those distributed elsewhere?; (3) is there evidence of an increased diversification rate in Western Amazonia after retreat of the Pebas system that could explain the higher species richness in this recently drained area compared with that in the older cratons (i.e. Brazilian and Guiana Shields)?

MATERIAL AND METHODS

TAXONOMIC SAMPLING AND MOLECULAR MARKERS

We sampled 29 out of 40 *Astrocaryum* spp. (72.5%) and the two *Hexopetion* spp., 2.4 times more *Astrocaryum* spp. than in the last molecular phylogenetic analysis of subtribe Bactridinae (Eiserhardt *et al.*, 2011b). We used 21 outgroup species representing tribes Cocoseae and Reinhardtieae (Baker *et al.*, 2009). We sequenced four nuclear loci: intron 4 of phosphoribulokinase (PRK; Lewis & Doyle, 2002), 3 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) and partial exon 1 of phytochrome B (PhyB; Ludeña *et al.*, 2011). The final combined data matrix consisted of 52 species and 3512 characters and is available in TreeBase study number 12088. A list of the sampled taxa, with voucher and GenBank accession numbers, is provided in Table 2. Laboratory methods for DNA extraction, amplification, cloning and sequencing followed those in Roncal *et al.* (2005), Bacon *et al.* (2008) and Ludeña *et al.* (2011). We cloned sequences that were unreadable or had a significant number of ambiguous base calls (18% of sequences generated for this study). We sequenced one to four clones for each sample. All clones from a taxon formed clades or were unresolved in individual gene tree analyses, and thus we selected the clone with the shortest branch length following the assumption that it most likely resembles the ancestor (Beilstein *et al.*, 2008).

Phylogenetic analyses and dating

We reconstructed the phylogeny of *Astrocaryum* using maximum parsimony (MP) and Bayesian methods. We conducted MP analysis in PAUP* 4.0b10 (Swofford, 2001), excluding uninformative characters and with equal character weighting. We performed an initial heuristic search of 1000 replicates, saving a maximum of 20 trees per replicate. We swapped to completion all trees recovered in the initial search, enforcing an upper limit of 25 000 optimal trees. We analysed clade support by calculating bootstrap values (BS) based on 1000 bootstrap replicates, each consisting of ten random searches, and saving no more than five trees in each step. For the combined Bayesian analysis in Mr Bayes 3.1.2 (Ronquist & Huelsenbeck, 2003), we executed two Markov chain Monte Carlo (MCMC) runs using a random starting tree, and ran 10 million generations, with a sampling frequency of one every 1000 generations. We discarded the first 2500 trees as burn-in, leaving a total of 17 500 trees. Prior to the Bayesian analysis, we used jModeltest 0.1.1 (Posada, 2008) on each data set to select the best-fit nucleotide substitution model and treat each gene partition separately. Under the Akaike information criterion (AIC) the general time-reversible model with a proportion of invariant sites and gamma-distributed rates (GTR + I + G), and the Hasegawa, Kishino, and Yano (HKY) model were selected for the PRK and RPB2 nuclear regions, respectively, whereas the HKY + G model was chosen for CISP4 and PhyB.

To estimate divergence times, we constrained the crown age of subtribe Attaleinae to 54.8 Mya, based on the fossil fruit from the middle to late Palaeocene of Colombia, which resembles extant *Cocos* (Gomez-Navarro *et al.*, 2009). This fossil was also selected for the molecular dating of the whole family (Couvreur *et al.*, 2011). Based on the fossil *Bactrites pandanifolius* Berry from the mid-Eocene of North America (Berry, 1924), we imposed a crown age of 40 Mya for subtribe Bactridinae. We used *Bactris pseudocuesco* Hollick and *Palmocarpon acrocomioides* Hollick to set the crown ages of *Bactris* Jacq. ex. Scop. and *Acrocomia* Mart. to 30 Mya (Hollick, 1928). As opposed to Eiserhardt *et al.* (2011b) and Meerow *et al.* (2009), who used these same fossils to calibrate the stems of the groups described, we used crown nodes, because affinities of these fossils to the constrained groups were unambiguous (Harley, 2006; Gomez-Navarro *et al.*, 2009) and the times when the synapomorphies appeared along the stem branches are unknown. To evaluate the influence of our choice on the results, we conducted an analysis, applying these calibrations to the stems, and found that divergence times for the selected clades (Table 3) were similar (–1.85 to 5.66 Myr different) to those obtained using the crowns. Ages fell within the 95% HPD of the crown calibration scheme (results not shown). The fifth and last fossil used was *Attalea olssoni* Berry from the Eocene/Oligocene of Peru (Berry, 1927) to set the stem age of *Attalea* to 35 Mya. To account for uncertainty in fossil ages, we used exponential prior distributions with offset at the age described for each fossil and a mean of 2. We used this distribution over the log-normal; as Ho (2007) suggested, it is appropriate for modelling fossil calibrations and because insufficient fossil information was available to describe the log-normal parameters. Finally, we set the a priori age of the root node using a normally distributed mean of 58 Mya and a standard deviation of 3 based on the divergence time split estimated between tribe Cocoseae and Reinhardtieae (Cuenca *et al.*, 2008). The dating analysis was conducted in BEAST V1.6.1 (Drummond & Rambaut, 2007). We performed a Bayes factor test in Tracer 1.5 to test whether the uncorrelated log-normal distribution of rates model fits the data significantly better than the strict molecular clock. We used the same nucleotide substitution models for the four data partitions as in the MrBayes analysis. We performed three independent runs of 1×10^7 generations sampled at frequency of 1/1000 using the Yule pure birth speciation model. We used the graphical exploration system of AWTY to check for convergence of the MCMC chains (Nylander *et al.*, 2008). We combined the BEAST log and tree files in LogCombiner 1.6.1 and summarized estimates of node ages and 95% highest posterior densities (HPD), discarding the first 3000 trees as burn-in in TreeAnnotator 1.6.1 (Drummond & Rambaut, 2007).

Ancestral area reconstruction and net diversification rate shifts

To reconstruct the ancestral areas of *Astrocaryum*, we conducted a maximum likelihood inference of geographical range evolution using the dispersal,

Table 2. List of taxa with voucher information (herbarium) and GenBank accessions for nuclear DNA sequences. 56 sequences were obtained from GenBank

Taxon	Voucher specimen	PRK	RPB2	CISP4	PHYB
Outgroup					
Allagoptera caudescens (Mart.) Kuntze	J. C. Pintaud 600 (G)	AY601244	JQ821997	JQ822031	JQ822070
Attalea phalerata Mart. ex Spreng	H. Balslev 6742 (AAU)	HQ265597	HQ265644	JQ822032	JQ822071
Beccariophoenix madagascariensis Jum. & H.Perrier	J. C. Pintaud 598 (G)	HQ265607	HQ265656	JQ822033	JQ822072
Butia eriospatha (Mart.) Becc.	L. Noblick 4879 (FTG)	JQ821972	–	JQ822034	JQ822073
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	W. Baker 1000 (FTG)	HQ265574	HQ265620	JQ822035	JQ822074
Acrocomia crispa (Kunth) C.F.Baker ex Becc.	J. Roncal 79 (FTG)	HQ265575	HQ265621	JQ822036	JF422042
Aiphanes minima (Gaertn.) Burret	S. Zona 873 (FTG)	HQ265581	HQ265627	JQ822037	JQ822075
Aiphanes horrida (Jacq.) Burret	F. Kahn & J. C. Pintaud 4500 (USM)	HQ265579	HQ265625	JQ822038	JQ822076
Bactris gasipaes Kunth	J. J. de Granville & Perthuis 17288 (CAY)	HQ265602	HQ265650	–	JQ822077
Bactris bifida Mart.	H. Balslev 7947 (AAU)	–	HQ265646	JQ822039	JQ822078
Desmoncus polyacanthos Mart.	H. Balslev 6620 (AAU)	HQ265612	HQ265660	JQ822040	JQ822079
Desmoncus orthacanthos Mart.	H. Balslev 6576 (AAU)	HQ265611	HQ265659	JQ822041	JF422044
Barcella odora (Trail) Drude	F. Kahn 3609 (CEN)	EF491112	JQ821998	JQ822042	JQ822080
Jubaeopsis caffra Becc.	J. C. Pintaud 597 (G)	HQ265615	HQ265663	JQ822043	JQ822081
Elaeis oleifera (Kunth) Cortés	H. Balslev 6555 (AAU)	AY601218	HQ265662	JQ822044	JQ822082
Cocos nucifera L.	Kew 1968–4480	HQ265608	EF491150	JQ822045	JQ822083
Voanioala gerardii J.Dransf.	J. Dransfield 6389 (K)	HQ265619	EF491153	JQ822046	JQ822084
Jubaea chilensis (Molina) Baill.	J. C. Pintaud 609 (G)	JQ821973	–	JQ822047	JQ822085
Parajubaea cocoides Burret	Cultivated at Kew	JQ821974	–	JQ822048	JQ822086
Lytocaryum weddellianum (H.Wendl.) Toledo	J. C. Pintaud 599 (G)	JQ821975	JQ821999	JQ822049	–
Reinhardtia simplex (H.Wendl.) Burret	C. Asmussen 4198_95 (NY)	HQ265617	HQ265665	JQ417546	–
Ingroup					
Astrocaryum acaule Mart.	R. Bernal 4377 (COL)	JQ821943	JQ821976	JQ822000	JQ822050
Astrocaryum aculeatum G.Mey	F. Kahn 3216 (P)	JQ821944	JQ821977	JQ822001	JQ822051
Astrocaryum campestre Mart.	H. Lorenzi 6535 (HPL)	JQ821946	JQ821978	JQ822003	–
Astrocaryum carnosum F.Kahn & B.Millán	F. Kahn 4476 (USM)	JQ821947	JQ821979	JQ822004	JQ822052
Astrocaryum chambira Burret	H. Balslev 7621 (AAU)	HQ265584	JQ821980	JQ822005	JF812601
Astrocaryum chonta Mart.	B. Millán 708 (USM)	JQ821948	JQ821981	JQ822006	JQ822053
Astrocaryum faranae F.Kahn & E.Ferreira	F. Kahn 4444 (USM)	JQ821949	JQ821982	JQ822007	JQ822054
Astrocaryum farinosum Barb. Rodr.	F. Kahn 3526 (CEN)	JQ821950	JQ821983	JQ822008	JQ822055
Astrocaryum ferrugineum F.Kahn & B.Millán	F. Kahn 3586 (CEN)	JQ821951	JQ821984	JQ822009	JQ822056
Astrocaryum gratum F.Kahn & B.Millán	B. Millán 558 (USM)	JQ821952	JQ821985	JQ822010	JQ822057
Astrocaryum gynacanthum Mart.	A. Pérez 934 (CAY)	JQ821953	HQ265632	JQ822011	JF422057
Astrocaryum huaimi Mart.	F. Kahn 4464 (USM)	JQ821954	EF491159	JQ822012	JQ822058

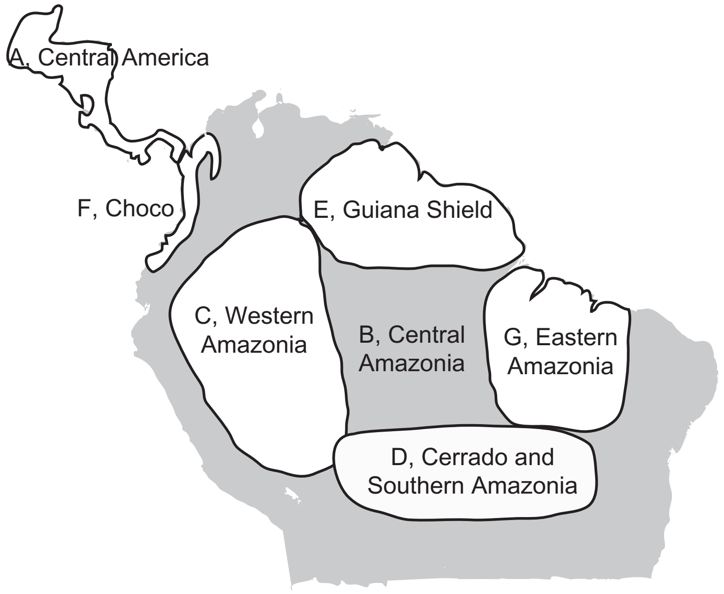
Table 2. *Continued*

Taxon	Voucher specimen	PRK	RPB2	CISP4	PHYB
Astrocaryum huicungo Dammer ex Burret	B. Millán 447 (USM)	JQ821955	JQ821986	JQ822013	JQ822059
Astrocaryum jauari Mart.	F. Kahn 610 (INPA)	JQ821956	JQ821987	JQ822014	JQ822060
Astrocaryum javarense (Trail) Drude	B. Millán 1087(USM)	JQ821957	JQ821988	JQ822015	JQ822061
Astrocaryum macrocalyx Burret	J. C. Pintaud 593 (USM)	JQ821958	JQ821989	JQ822016	JQ822062
Astrocaryum malybo H.Karst	N. D. Jiménez 109 (COL)	JQ821959	HQ265634	JQ822017	JF422059
Astrocaryum minus Trail	J. de Granville 17666 (CAY)	JQ821961	HQ265636	JQ822019	JQ822063
Astrocaryum murumuru Mart.	A. Pérez 718 (CAY)	JQ821962	HQ265637	JQ822020	JF422046
Astrocaryum paramaca Mart.	A. Pérez 787 (CAY)	JQ821963	JQ821990	JQ822021	JF422048
Astrocaryum perangustatum F.Kahn & B.Millán	B. Millán & F. Kahn 1597 (USM) F. Kahn 4439 (USM)	JQ821964	JQ821991	JQ822022	JQ822064
Astrocaryum rodriguesii Trail	J. J. de Granville & G. C 12801 (CAY)	JQ821965	JQ821992	JQ822023	JF422049
Astrocaryum sciophilum Miq. (Pulle)	J. J. de Granville 11074 (CAY)	JQ821966	JQ821993	JQ822024	JF422047
Astrocaryum scopatum F.Kahn & B.Millán	F. Kahn 4340 (USM)	JQ821967	JQ821994	JQ822025	JQ822065
Astrocaryum sociale Barb. Rodr.	F. Kahn 3617 (USM)	JQ821968	JQ821995	JQ822026	JQ822066
Astrocaryum standleyanum L.H.Bailey	I. Suarez 006 (QCA)	HQ265594	HQ265641	JQ822027	JQ822067
Astrocaryum ulei Burret	F. Kahn 4460 (USM)	JQ821969	JQ821996	JQ822028	JQ822068
Astrocaryum urostachys Burret	F. Kahn 4347 (USM)	JQ821970	HQ265642	JQ822029	JF422051
Astrocaryum vulgare Mart.	L. Noblick 4972 (FTG)	JQ821971	HQ265643	JQ822030	JQ822069
Hexopetion alatum Loomis	S. Zona 921 (FTG)	JQ821945	HQ265630	JQ822002	JF422040
Hexopetion mexicanum Liebm.	J. C. Pintaud 637 (USM)	JQ821960	HQ265635	JQ822018	JF812602

Table 3. Mean crown node ages and 95% highest posterior densities (HPD) for selected clades compiled from 27 001 trees in the Bayesian posterior distribution using a relaxed clock model in BEAST based on a data set of 3.5 kb of nuclear DNA

Clade	Mean age (Mya)	95% HPD
Bactridinae	43.1	40–47.2
Bactris/Hexopetion/Astrocaryum	36.5	33.6–40.2
Hexopetion/Astrocayum	33.2	26.4–38.6
Astrocaryum	20.6	14.6–27.7
Astrocaryum chambira	15.9	11.2–21.6
Node of diversification rate shift	13.4	9.7–18.3
Subgenus *Munbaca*	6.5	3.8–9.7
Section *Monogynanthus*	3.4	1.3–6.4
Section *Huicungo*	6.3	4.0–9.2

extinction and cladogenesis (DEC) model implemented in LAGRANGE build 20110117 (Ree & Smith, 2008). We chose this approach over dispersal–vicariance analysis (Ronquist, 1997), because it considers within-range speciation scenarios and time-calibrated branch lengths, and does not favour vicariance, especially at inner nodes (Buerki *et al.*, 2011). Seven geographical areas were delimited on the basis of the palaeogeography of tropical America, extant floristic regions and distributions of *Astrocaryum* spp. (Fig. 1): Central America (area A), central Amazonia (area B), western Amazonia including the eastern Andean piedmont (area C), cerrado and southern Amazonia periphery (area D), Guiana Shield (area E), Chocó region and northern Colombian inter-Andean valleys (area F) and eastern Amazonia (area G). We did not include the Brazilian coastal Atlantic rainforest in this analysis, because we were not able to amplify DNA of the single endemic species from that



A. Biogeographical regions

B. Complex palaeogeographical model

Time frame 1: from 33 to 22 myr

	A	**B**	**C**	**D**	**E**	**F**	**G**
A	0						
B	0.1	0					
C	0.1	1	0				
D	0.1	1	1	0			
E	0.1	1	1	0.5	0		
F	1	0.5	1	0.5	0.1	0	
G	0.1	1	0.5	1	1	0.33	0

Time frame 2: from 22 to 11 myr

	A	**B**	**C**	**D**	**E**	**F**	**G**
A	0						
B	0.1	0					
C	0.1	0.1	0				
D	0.1	1	0.1	0			
E	0.1	0.1	0.1	0.1	0		
F	0.5	0.1	0.1	0.1	0.1	0	
G	0.1	1	0.1	1	0.1	0.1	0

Time frame 3: from 11 myr to date

	A	**B**	**C**	**D**	**E**	**F**	**G**
A	0						
B	0.01	0					
C	0.01	1	0				
D	0.01	1	1	0			
E	0.01	0.1	1	0.1	0		
F	1	0.01	0.01	0.01	0.01	0	
G	0.01	1	0.5	1	0.1	0.01	0

Figure 1. (A), biogeographical areas used in the study of *Astrocaryum*. (B), palaeogeographical model with three time frames reflecting the probability of dispersal across areas through time.

region (*A. aculeatissimum* Burret). The Andean mountains > 1000 m elevation were also not included as a biogeographical area, because they fall outside the distribution of *Astrocaryum*. Each *Astrocaryum* sp. and *Hexopetion* sp. was assigned to one or more geographical areas according to their distribution (Kahn, 2008), with two species occurring in a maximum of four areas. We selected the *Astrocaryum*/*Hexopetion* clade from the BEAST maximum clade credibility tree to reconstruct ancestral areas, because this group and not the entire subtribe was the focus of our research. Allowing an ancestral range of maximum four areas rendered a widespread *Astrocaryum* ancestor occurring in the Guiana Shield, Chocó, western Amazonia and the cerrado (results not shown). This most likely widespread reconstruction was obtained for basal nodes of the tree until *c.* 11 Mya (except for the ancestor of *Hexopetion* and *A. chambira* Burret). We considered it unlikely that the ancestor of *Astrocaryum* would be adapted to grow in such wide environmental conditions, i.e. the Chocó and cerrado, and not be present in central Amazonia, and we thus constrained the maximum ancestral range size to three areas in our biogeographical model.

We conducted two biogeographical analyses. First, we defined a null hypothesis in which all geographical areas are adjacent with no spatial constraint through time, and thus with equal rates of dispersal (values of 1) among all possible geographical areas. Alternatively, we defined a more complex palaeogeographical hypothesis with different spatial and temporal dispersal constraints. We stratified the *Astrocaryum*/*Hexopetion* phylogenetic tree into three time frames and elaborated a dispersal cost matrix for each one of them, reflecting the American palaeogeographical changes during the last 33 Myr (Fig. 1). Time frame 1 (33 to 22 Mya) experienced a lack of connectivity between South and Central America, therefore we scaled down the dispersal probability across Central America to 0.1. We did not use a lower cost value because transoceanic dispersal in palms has been reported (Gunn, 2004; Bjorholm *et al.*, 2006; Trénel *et al.*, 2007; Cuenca *et al.*, 2008; Meerow *et al.*, 2009; Bacon *et al.*, 2012a). We also assigned a dispersal constraint of 0.1 between the Guiana Shield and the Chocó because of the presence of the Palaeo-Orinoco river during time period 1 (Antonelli & Sanmartin, 2011). We used a value of 0.5 for the dispersal across non-adjacent areas separated by two steps and no other geological constraint (e.g. between western and eastern Amazonia), and a value of 0.33 between the Chocó and eastern Amazonia because three steps are necessary.

Lake Pebas posed a colonization constraint in western Amazonia during time frame 2 (22–11 Mya), and thus dispersal to or across this area was set to 0.1. Similarly, the precursor of the Amazon river, hypothesized to be a fluvio-lacustrine system with an eastward direction (Hoorn *et al.*, 1995; Graham, 2010), led us to constrain dispersal across it by a factor of 0.1. The tropical Andes did not pose a major dispersal barrier during this time period because they were only approximately half their current elevation (Gregory-Wodzicki, 2000). We set a dispersal constraint of 0.5 between Central and South America because of the proposed presence of a land bridge (*c.* 8.5–14 Mya; Iturralde-Vinent & MacPhee, 1999) and an initial fracturing of the Panamanian isthmus during collision with South America dated at 23–25 Mya (Farris *et al.*, 2011).

A value of 0.01 was attributed to the dispersal across the Andes during time frame 3 (11 Mya to present) because the Andean mountains reached sufficient heights to act as an effective dispersal barrier. We applied a dispersal cost of 0.1 across the Amazon. Migration between Central and South America was allowed during time frame 3 because of a hypothesized archipelago (9–7 Mya; Coates & Obando, 1996), a short-lived terrestrial corridor (*c.* 4–7 Mya; Bermingham & Martin, 1998) and the closure of the Panamanian isthmus.

To detect temporal shifts in diversification rates in the Bactridinae phylogeny, we used turboMEDUSA (Alfaro *et al.*, 2009), an algorithm that fits multiple birth–death models to an ultrametric tree, taking into account incomplete taxon sampling, and using a stepwise AIC approach to determine optimal model size. We pruned the BEAST chronogram to include one lineage for *Desmoncus* Mart. (seven species), *Acrocomia* (three species), *Aiphanes* (24 species), *Bactris* (77 species) and *Astrocaryum* section *Huicungo* F.Kahn (15 species). A taxonomic richness matrix was prepared with these lineages, all *Astrocaryum* spp. outside section Huicungo, and assigning nine of the 11 missing *Astrocaryum* taxa to their closest relative(s) based on morphology (Kahn, 2008). For example, *A. ciliatum* F.Kahn & B.Millan and *A. cuatrecasanum* Dugand were allocated to section Huicungo, *A. confertum* H.Wendl. ex Burret was linked to *A. standleyanum* L.H.Bailey, *A. echinatum* Barb.Rodr. was linked to *A.vulgare* Mart., *A. giganteum* Barb.Rodr. was linked to *A. acaule* Mart., and *A. arenarium* Barb.Rodr., *A. kewense* Barb.Rodr., *A. pygmaeum* Drude, *A. weddellii* Drude were linked to *A. campestre* Mart. We had no a priori basis to assign a lineage for *A. triandrum* Galeano, R.Bernal & F.Kahn and *A. aculeatissimum*, and thus these were excluded from the analysis. Using the corrected for small sample size Akaike information criterion (AICc), we compared a homogeneous birth–death model over the Bactridinae phylogeny with other models containing one or multiple shifts in diversification and relative extinction rates. We acknowledge that, by collapsing branches, we lose resolution in incompletely sampled groups, but we were interested in detecting a shift in diversification rate at the crown of section *Huicungo*, not within this group. Our analysis does not discard the possibility of additional shifts in diversification rates in those collapsed lineages, but that was outside the scope of this paper.

RESULTS

Phylogenetic analyses and dating

The concatenated data matrix contained 480 potentially parsimony informative characters (13.67% of total). Maximum parsimony analysis resulted in 26 most-parsimonious trees of length 857, a consistency index (CI) 0.67, retention index (RI) 0.87 and rescaled consistency index (RC) 0.58. Parsimony strict consensus and Bayesian 50% majority rule consensus trees were concordant, and phylogenetic relationships recovered among genera of Cocoseae were largely in agreement with previous molecular studies (Fig. 2; Gunn, 2004; Meerow *et al*., 2009; Eiserhardt *et al*., 2011b). *Hexopetion* and *Astrocaryum* formed a moderately supported clade with posterior probability (PP) of 0.84 and bootstrap support (BS) of 73. Both genera were monophyletic with PP of 1 and BS of 100% (Fig. 2). A clade consisting of *A. huaimi* Mart., *A. jauari* Mart. and *A. acaule* was sister to all other *Astrocaryum* spp. (PP = 1, BS = 62). Resolution among the remaining *Astrocaryum* spp. was not fully attained, but several clades were recovered. Members of subgenus *Munbaca* were monophyletic (PP = 1, BS = 88) and were sister to the monophyletic subgenus *Monogynanthus* section *Monogynanthus* (PP = 1, BS = 100), both clades distributed in the Guiana Shield and Central Amazonia. Another clade consisted of species occurring mostly in western Amazonia (subgenus *Monogynanthus* section *Huicungo*, PP = 1, BS = 98). Our results thus indicate that subgenus *Munbaca* is monophyletic, but subgenera *Astrocaryum* and *Monogynanthus* were paraphyletic as circumscribed by Kahn (2008).

The BEAST maximum clade credibility tree was similar in topology to that obtained from the MrBayes analysis. *Astrocaryum minus* Trail was sister to *A. gynacanthum* Mart. in BEAST, whereas *A. minus* appeared as sister to *A. paramaca* Mart. and *A. rodriguesii* Trail in MrBayes. *Astrocaryum huicungo* Dammer ex Burret was sister to *A. ferrugineum* Kahn & Millan in BEAST, but sister to a clade of *A. scopatum* Kahn & Millan/*A. chonta* Mart./*A. ulei* Burret in MrBayes. These incongruent relationships were supported with PP < 0.74. Mean divergence times and 95% highest posterior densities (HPD) of selected nodes are presented in Table 3, and the chronogram of the full taxonomic sampling including fossil calibration points is shown in Figure 3. The split between *Astrocaryum* and *Hexopetion* was estimated at *c*. 33.2 Mya. Divergence of *A. chambira*, currently distributed in western Amazonia, was estimated during the presence of the Pebas system at *c*. 15.9 Mya, whereas diversification of section *Huicungo* occurred after the retreat of this system, *c*. 6.3 Mya.

Ancestral area reconstruction and net diversification rate shifts

The ancestral range reconstruction obtained under the DEC model approach plotted on the BEAST chronogram of *Hexopetion*/*Astrocaryum* is shown in Figure 4. The DEC model supported an ambiguous inherited range for *Astrocaryum* at the split with *Hexopetion*. The range composed of the Guiana Shield and western Amazonia received the highest relative probability (RP = 0.15), whereas the Guiana Shield alone had the second-highest probability (RP = 0.13). The ancestral distribution for *Hexopetion* was Central America (RP = 0.81). During time frame 2 (22–11 Mya) branches also had ambiguous range reconstructions, with the Guiana Shield receiving the highest RP in all branches (0.14–0.55), except for the branch that leads to *A. chambira* (RP for western Amazonia was 0.61, whereas for the Guiana Shield it was only 0.16). Most cladogenesis events in *Astrocaryum* occurred during time frame 3 (11 Mya to date), with several range expansions or colonizations. Two colonization events from most likely the Guiana Shield to the cerrado (by *A. campestre*) and the southern periphery of Amazonia (by *A. huaimi*) took place. The ancestor of the clade formed by subgenus *Munbaca* and section *Monogynanthus* (*A. sciophilum* to *A. minus* in Fig. 4) had an ancestral range in the Guiana Shield (RP = 0.90), and subsequently expanded into eastern, central and western Amazonia. Two other dispersals from most likely the Guiana Shield to Central America and the Choco (*A. standleyanum* and *A. malybo* H.Karst.) occurred also during the third time period. The ancestor of section *Huicungo* originated in western Amazonia (RP = 57) or in the Guiana Shield (RP = 31) and some species in this clade expanded their ranges into central, southern and eastern Amazonia (Fig. 4).

Results from the null model were similar to those of the complex biogeographical cost model, except for four branches that showed a different most probable ancestral area (see also Supporting Information, Fig. S1). In all four cases, the Guiana Shield was recovered as the most likely ancestral distribution over alternative regions, comprising the Guiana

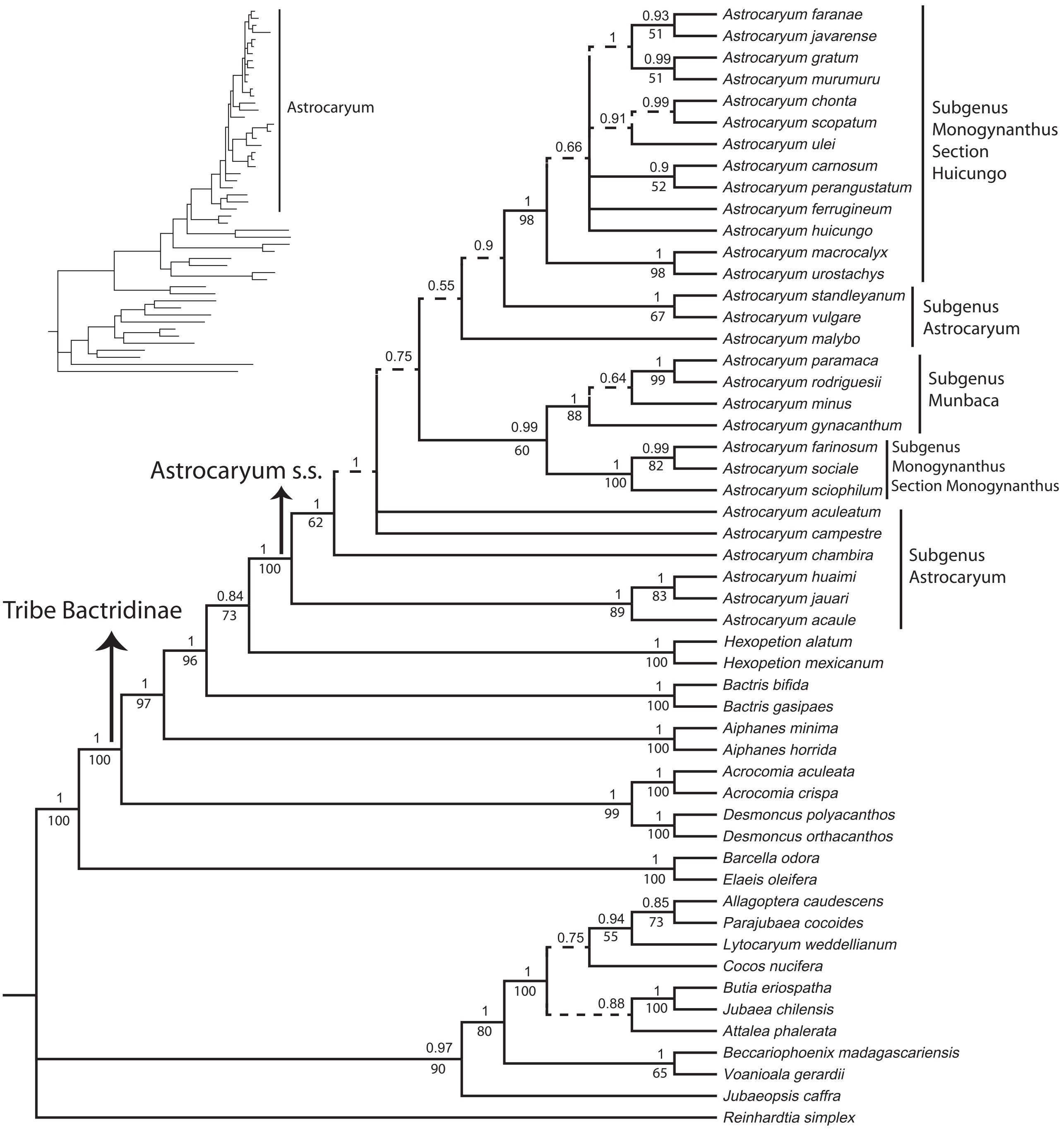


Figure 2. Bayesian 50% majority rule consensus tree of *Astrocaryum* and outgroup taxa resulting from a combined analysis of 3.5 kb of nuclear DNA. Values above branches are the posterior probabilities, and values below branches are the maximum parsimony bootstrap support. Dashed lines collapse in the parsimony strict consensus tree. Inset is the Bayesian phylogram showing branch lengths.

Shield plus western Amazonia, central Amazonia and the Choco. Using the null model, 17 branches showed increased probability for the Guiana Shield as ancestral area, and dispersal events were not in conflict with the palaeogeographical information. The null model received a lower likelihood than the biogeographical model (null model –lnL = 95.34, biogeographical model –lnL = 85.01).

One diversification rate shift was identified using turboMEDUSA located at the split between the clade

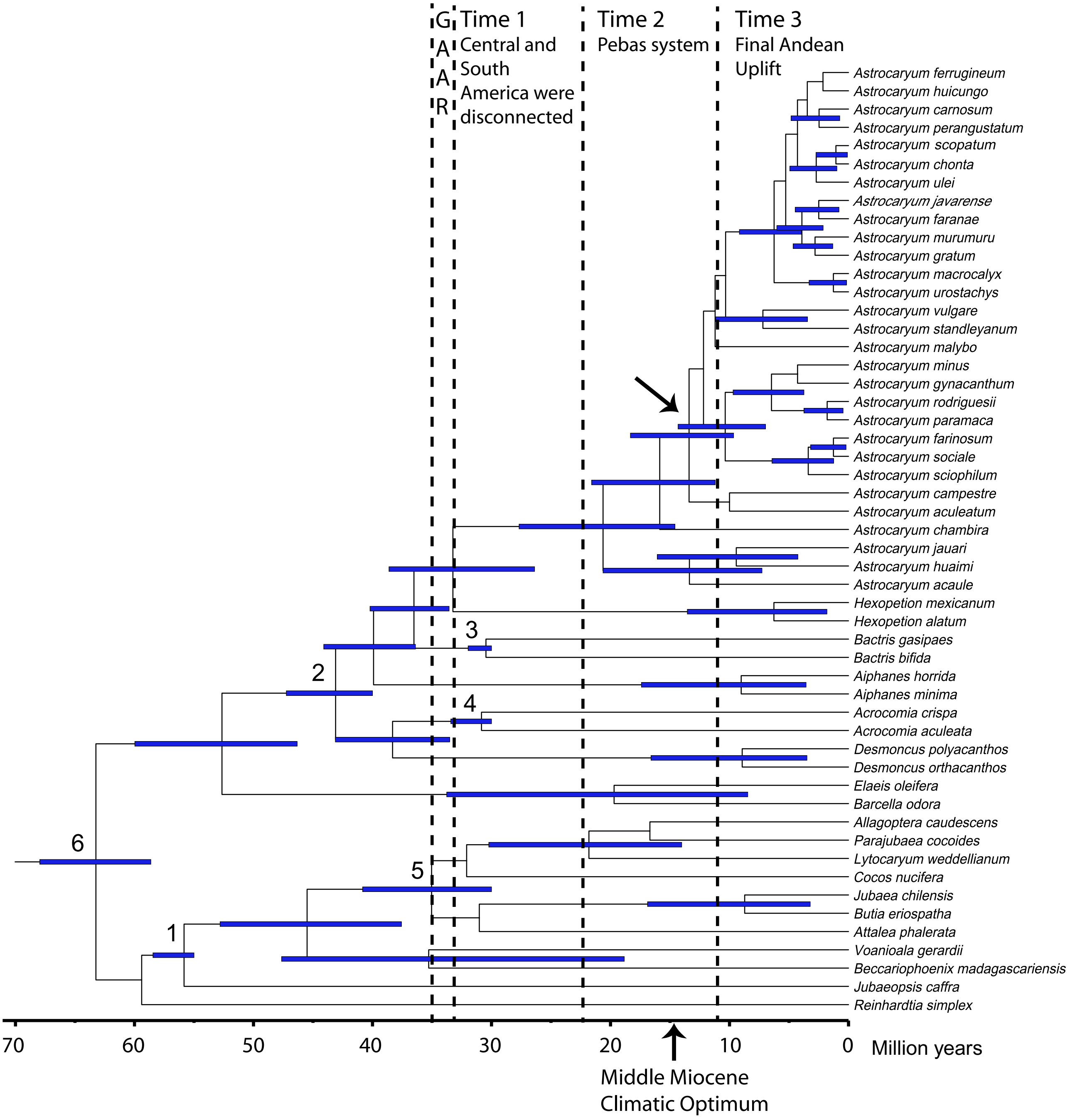


Figure 3. Maximum clade credibility chronogram of *Astrocaryum* obtained from the Bayesian dating analysis in BEAST using 3.5 kb of nuclear DNA. Bars represent the 95% highest posterior densities for those nodes supported with posterior probabilities > 0.9 in the phylogenetic reconstruction of BEAST. Numbers at nodes are calibration points: 1, *Cocos* fossil constrained the crown age of subtribe Attaleinae at 54.8 Mya (exponential prior distribution with mean of 2 used in all fossil calibrations); 2, *Bactrites pandanifolius* set the crown age of subtribe Bactridinae at 40 Mya; 3, *Bactris pseudocuesco* constrained the crown age of *Bactris* at 30 Mya; 4, *Palmocarpon acrocomioides* constrained the crown age of *Acrocomia* at 30 Mya; 5, *Attalea olssoni* constrained the stem age of *Attalea* to 35 Mya; 6, root node set at 58 ± 3 Mya (normally distributed mean ± standard deviation). Time frames with main geological events used in the biogeographical reconstruction are indicated, as well as the formation of GAARlandia between 35–33 Mya. Arrow indicates point of net diversification rate increase coinciding with the mid-Miocene climatic optimum.

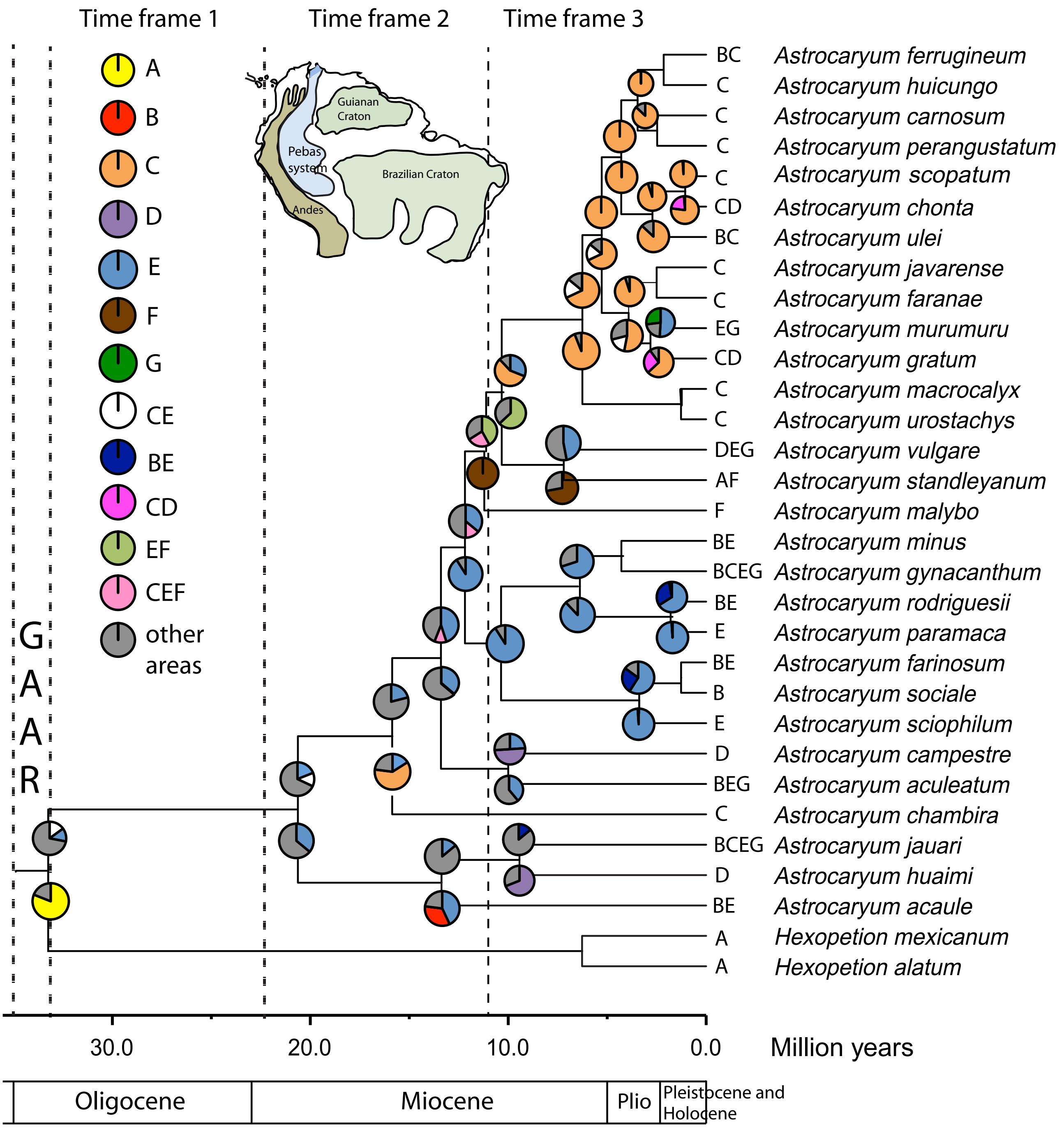


Figure 4. Reconstruction of geographic range evolution inferred by a dispersal, extinction and cladogenesis (DEC) model in Lagrange with dispersal restrictions according to Figure 1B. Results plotted into the BEAST maximum clade credibility chronogram. Pie charts on branches represent relative probabilities of alternative ranges inherited, grey sections represent all other areas with relative probabilities < 0.1. Extant area distribution for each species is indicated before species names. Area coding and circumscription as in Figure 1. Vertical dashed lines represent the time boundaries of GAARlandia and the three time frames. Inset is map of South America showing presence of the Pebas system from *c.* 22 to 11 Mya (modified from Hernandez *et al.*, 2005). Geological timescale from the International Commission on Stratigraphy of 2009.

of *A. campestre* and *A. aculeatum,* and its sister clade at *c.* 13.4 Mya (Fig. 3). There was a twofold increase in the diversification rate (r) at this point with respect to the earlier part of the chronogram, whereas the extinction rate (e) decreased tenfold ($r_1 = 0.089$, $e_1 = 3.61e\text{-}06$, $\mathrm{lnlik}_1 = -51.88$; $r_2 = 0.179$, $e_2 = 3.66e\text{-}07$, $\mathrm{lnlik}_2 = -43.71$). This selected model had an AICc of 202.7, AICc weight of 0.59, log-likelihood of –95.58 and five parameters. The second-best model was the homogeneous birth–death, which received an AICc of 203.8, AICc weight of 0.34, log-likelihood of –99.78 and two parameters. All other models were much less informative as they received an AICc weight of < 0.07 and are thus not reported. Estimated values for the homogeneous birth–death model were $r = 0.096$ and $e = 0.257$.

DISCUSSION

Phylogenetic, dating and biogeographic analyses

As in Eiserhardt *et al*. (2011b), phylogenetic analysis of PRK, RPB2, CISP4 and PhyB nuclear regions supported the sister relationship of *Hexopetion* to *Astrocaryum*. *Hexopetion* could be considered a subgenus or genus, leaving this a matter of taxonomic scale concept. Divergence times were concordant with dates obtained in previous studies focusing on subtribes Bactridinae and Attaleinae and tribe Cocoseae (Gunn, 2004; Meerow *et al*., 2009; Eiserhardt *et al*., 2011b). The divergence of *Hexopetion*/*Astrocaryum* from *Bactris* was estimated to occur at *c.* 33 Mya (HPD = 30–38, calibration scheme B) and the crown age of *Hexopetion*/*Astrocaryum* was *c.* 30 Mya (HPD = 23–36) in the reconstruction of tribe Bactridinae (Eiserhardt *et al*., 2011b), whereas we obtained 36.5 (HPD = 33–40) and 33.2 (HPD = 26–39) Mya, respectively. Discrepancies in age estimations attributable to differences in taxon sampling density have been shown for Restoniaceae (Linder, Hardy & Rutschmann, 2005); our older dates relative to those found in Eiserhardt *et al*. (2011b) could thus be explained by the increased taxon sampling or by the different calibration constraints. The most recent common ancestor of American Attaleinae had a mean age of 38.4 Mya (HPD = 25–45 Mya) in the analysis of subtribe Attaleinae (Meerow *et al*., 2009), whereas in our ultrametric tree this node was 35 Mya (HPD = 30–41). Gunn's (2004) study of tribe Cocoseae found a divergence time of the 'spiny' clade (Bactridinae and *Elaeis*) at 46 Mya, whereas our analysis recovered an age of *c.* 52.7 Mya (HPD = 46–60).

One of the limitations of the DEC approach implemented in LAGRANGE is the use of a single phylogenetic tree that ignores phylogenetic uncertainty in the biogeographic reconstruction. Most of the nodes in the phylogenetic tree received high support (Fig. 2), but, for those that collapse in the strict consensus MP tree, the recovered ancestral areas await confirmation upon availability of a better-resolved species tree. Another limitation of this method is the definition of a cost matrix. We assessed the robustness of our results by running a null model of equal dispersal probability across areas. Most reconstructed areas were equal (Fig. 4; see also Supporting Information, Fig. S1) and conclusions of our analysis (discussed below) are the same using both models. This suggests that the palaeogeographic events we used to constrain dispersal of *Astrocarym* lineages might have played a small role in their distribution. It has been shown that divergence times and phylogenetic uncertainties influence the inference and decisiveness of ancestral range reconstruction (Buerki *et al*., 2011). The high indecisiveness of the biogeographical reconstruction at the basal nodes of our tree could be attributed to this uncertainty or to the widespread ranges of terminal taxa.

As suggested for many other plant lineages, the Greater Antilles and the Aves Ridge (GAARlandia, 33–35 Mya) might have facilitated dispersal of the ancestor of *Hexopetion* / *Astrocaryum* between Central and South America during the Eocene–Oligocene boundary (Iturralde-Vinent & MacPhee, 1999), because its crown node age coincides with the formation of this land bridge (Table 3). Deciphering whether this ancestor had a Central or South American distribution requires a biogeographical study on a broader taxonomic scale. If this ancestor had a South American distribution, as suggested for Arecoideae (Baker & Couvreur, in press-a, b), then two independent colonization events into Central America would be revealed by our ultrametric tree, one by *Hexopetion* (later than 38.6 Mya), and the other by *A. standleyanum* (later than 11 Mya). GAARlandia has also been proposed as a land bridge that enabled migration of *Copernicia* (Trachycarpeae: Arecaceae) to the Antilles and South America from North America (Bacon *et al*., 2012a).

The Pebas system

Current high species richness in western Amazonia can be attributed, at least in part, to the edaphic heterogeneity of the Pebas formation (Wesselingh & Salo, 2006). Palaeontological, geological and biogeographical evidence must be gathered to advance our knowledge on the configuration of the Pebas system and its influence on species diversity in the region. According to Latrubesse *et al*. (2010), no evidence of marine influence exists in the faunal fossil record, and the isotopic composition of molluscan shells points to a very limited influx of marine waters (Vonhof *et al*., 2003). However, indicators of marine influence include dinoflagellates, pollen from mangrove trees and marine ichnofossils that thrived in the wetland (Hoorn *et al.*, 2010). The fossil vertebrate record from Acre, Brazil is compatible with a large flooded basin that includes shallow lakes, grasslands, river swamps, river-edge or lake-side gallery forests subject to seasonal floods in a tropical wet–dry climate (Latrubesse *et al.*, 2010). Recent sedimentological observations from the Solimoes formation confirm the fluvial model (Gross *et al.*, 2011).

To date, few molecular phylogenetic or biogeographical studies have addressed the influence of Pebas on the diversification dynamics and distribution patterns of Neotropical plant lineages (Antonelli *et al.*, 2009). Our biogeographical analysis showed that the ancestor of the western Amazonian section *Huicungo* started cladogenesis approximately 6 Mya (HPD = 4–9), and diversified into 15 species during the fast and final period of Andean orogeny after subsidence of Pebas (Fig. 4). This is concordant with evidence from species-rich tree genera, such as *Inga* (Richardson *et al.*, 2001) and *Guatteria* (Erkens *et al.*, 2007), the recent divergence times of which (< 10 Mya) suggest speciation occurred after retreat of Pebas and favour the hypothesis of a mega-lake system that inhibited colonization and *in situ* speciation. Similarly, in the palm genus *Geonoma*, species endemic to western Amazonia (nine species) did not form a clade and their diversification times were < 8 Mya (Roncal *et al.*, 2011), also indicating that diversification of these species occurred after the Pebas drained. Palynological evidence has also evoked an increase in plant diversity of 10–15% after forests replaced wetlands (Hoorn *et al.*, 2010).

Our reconstruction also showed that *Astrocaryum chambira* originated during the Pebas and either did not diversify further even after drainage of the aquatic system or it is the sole survivor of its lineage (Fig. 4). This finding supports the river hypothesis sectioned by gallery or terra firme forests where ancestors, such as that of *A. chambira*, could have originated and subsequently occupied drained habitats in western Amazonia. However, an accurate biogeographical reconstruction that could provide insight into the configuration of the Pebas system is challenging because of post-speciation dispersals to western Amazonia from adjacent areas (Pennington & Dick, 2010) and would perhaps require a fine-scale phylogeographic approach. Analysis of a much wider spectrum of lineages is clearly needed to validate one of the Pebas hypotheses. An extensive search of 168 molecular phylogenetic studies of tropical insects, mammals, amphibians, birds and plants showed that diversification in 68% of the lineages occurred < 10 Mya (Hoorn *et al.*, 2010), which agrees with the hypothesis that most diversification in northern South America occurred after the retreat of the Pebas.

THE GUIANA SHIELD

Extant *Astrocaryum* spp. distributed in the Guiana Shield did not form a clade, and post-speciation dispersals challenge the interpretation of an early branching position for Guiana species. The mean stem age estimate for *Astrocaryum* was 33.2 Mya (HPD = 26–39), and this ancestor most likely occupied the Guiana Shield–western Amazonia region, as revealed in the LAGRANGE analysis (Fig. 4). The cladogenesis events that followed until the end of the Pebas system most probably developed in the Guiana Shield, except for divergence of *Astrocaryum chambira* in western Amazonia. The ancestral distribution of *Astrocaryum* in the Guiana Shield during time frames 1 and 2 suggests this area acted as a source from where *Astrocaryum* spp. colonized adjacent areas in tropical America. Range expansions of western Amazonian species to eastern, central and southern Amazonia occurred more recently, in the last 6 Myr.

Phylogenetic analyses of plant and animal lineages corroborate the hypothesis of a long-term occupation of the Guiana Shield, from where species dispersed to other areas. For example, bromeliads arose in the Guiana Shield *c.* 100 Mya (Givnish *et al.*, 2011). Using Amazonian *Charis* butterflies as a case study, Hall & Harvey (2002) proposed an area cladogram supporting an historical vicariant split between Guiana and the remainder of Amazonia, and then between the upper and lower Amazon. Some of the oldest lineages in the poison frog family, Dendrobatidae, originated in the Guiana Shield and Venezuelan highlands, with the oldest vicariant event in this family occurring in the latter region (Santos *et al.*, 2009). Evidence from Amazonian birds indicated that lineages in western Amazonia are associated with more basal lineages from the Brazilian Shield, the Guiana Shield and the Andes (Aleixo & de Fatima Rossetti, 2007). In a comparison of area cladograms across amphibians, reptiles, birds, primates, rodents/marsupials and butterflies, the Guiana clade consistently appeared at the base of all other areas or as sister to an upper Amazon clade (Hall & Harvey, 2002).

AN INCREASED DIVERSIFICATION RATE IN THE WESTERN AMAZONIAN CLADE?

Significant changes in speciation and extinction rates correlated with geological or climatic events may elucidate the dynamics of community turnover through geological time. It has been hypothesized that diversification in western Amazonia must have been rapid after the retreat of the Pebas system, because species richness in this area is higher than that of the older cratons (Hoorn *et al.*, 2010). Our results showed an increased diversification rate for a clade that is not restricted to western Amazonia, but for a clade the ancestor of which most likely occupied the Guiana Shield (Fig. 4). This clade has a crown node age during the Pebas system (*c*. 13 Mya, HPD = 10–18). This point of increased diversification rate coincides temporally with the climate cooling after the mid-Miocene climatic optimum (17–15 Mya; Zachos *et al*., 2001). The late Miocene was a period of climatic cooling and drying (Zachos *et al*., 2001), which might have influenced the reproduction, establishment and growth of individuals and, consequently, community assembly. It was during this period that the establishment of modern fire regime and the expansion of C4 grasslands occurred (Keeley & Rundel, 2005; Graham, 2010, 2011). In a study of the assembly processes of western Amazonian palm communities, Eiserhardt *et al*. (2012) found that environmental filtering into major habitats played the most important role, followed by biogeographical and within-habitat processes.

An opportunistic immigration to new open habitats triggered by the mid-Miocene climatic optimum, with subsequent species diversification, has been proposed for several taxa in the Southern Hemisphere. These include *Pseuduvaria* Miq. (Annonaceae) in Asia (Su & Saunders, 2009), *Hoffmannseggella* H.G.Jones (Orchidaceae) in Brazil (Antonelli *et al*., 2010), *Disa* P.J.Bergius (Orchidaceae) in South Africa (Bytebier *et al*., 2011) and *Licuala* Wurmb (Arecaceae) in Australia (Crisp *et al*., 2010). The point of increased diversification rate found in *Astrocaryum* could be similarly explained by the evolution of fire-adapted cerrado species (six species) and by the diversification of species with different growth forms in the Guiana Shield and central Amazonia (clade of seven species) and the allopatric speciation of the western Amazonian clade (15 spp.). We hypothesize that most *Astrocaryum* spp. growing in the cerrado have developed a grass-like fire-resistant habit *in situ*, as is the case of several other cerrado plant lineages (Simon *et al*., 2009). The clade corresponding to subgenus *Munbaca* and section *Monogynanthus* grows in the Guiana Shield and central Amazonia and comprises species with four of the eight palm growth forms recently recognized by Balslev *et al*. (2011). These four growth forms can be found in sympatry, exploiting different niches. Finally, the point of increased diversification is also concurrent with the Andean upheaval and subsequent formation of ridges and arches in Amazonia (Räsänen *et al*., 1990). These geological events likely caused vicariant speciation of the western Amazonian clade (section *Huicungo*) by isolation of populations into different inter-Andean valleys, Amazonian river basins and ecological niches (Kahn *et al*., 2012). Overall diversification patterns in *Astrocaryum* are similar to those found in riodinid butterflies (Hall & Harvey, 2002).

Other empirical studies have reported changes in diversification rates correlated with periods of past global warming or cooling and Andean upheaval. For example, Jaramillo, Rueda & Mora (2006) and Jaramillo *et al*. (2010) found increased floristic diversity and diversification rates during the Paleocene Eocene thermal maximum (*c*. 56 Mya) based on fossil pollen data from Colombia and Venezuela. Palynological evidence has shown higher plant diversity near the end of the mid-Miocene climatic optimum, but still lower than that in the Palaeogene (Hoorn *et al*., 2010). In their study of poison frogs, Santos *et al*. (2009) documented a decreased diversification rate for Andean species since the mid-Oligocene, potentially explained by their failure to adapt to Andean-caused dramatic ecological changes. However, diversification was intensified in the Andean–lowlands interface during the Pliocene, as in *Astrocaryum*.

CONCLUSIONS AND FUTURE RESEARCH PROSPECTS

The biogeographical evidence based on dated molecular phylogenies supports the hypothesis of a Pebas wetland system that inhibited *in situ* speciation in western Amazonia, because divergence times of several plant and animal clades (including *Astrocaryum* section *Huicungo*) post-dated the drainage of Pebas (< 10 Mya). The most likely ancestral distribution of *Astrocaryum* until retreat of the Pebas system is the Guiana Shield, suggesting that this old formation acted as a source from which *Astrocaryum* spp. colonized adjacent areas in tropical America. Post-speciation dispersals challenge the interpretation of an earliest branching position for Guiana *Astrocaryum* spp., but area cladograms from birds, primates, rodents/marsupials and butterflies recovered an earliest branching Guiana clade (Hall & Harvey, 2002). We found a twofold increase in diversification rate for a clade, the ancestor of which occupied the Guiana Shield, and not just for the western Amazonian clade, and temporally coinciding with the cooling after the mid-Miocene climatic optimum and the onset of a major phase of Andean uplift (*c*. 13 Mya).

As molecular phylogenetic reconstruction and dating techniques become more accurate, biogeographical reconstructions will also more reliably infer range evolution and speciation/extinction dynamics, especially in the light of new methodologies (Ree & Sanmartin, 2009; Morlon, Parsons & Plotkin, 2011). Future biogeographical analyses of additional plant and animal lineages endemic to the Neotropics and meta-analyses will shed light on the influence each palaeogeographical event had on species diversification in space and time. In addition, results of these analyses could support or reject some of the contentious palaeogeographical hypotheses for tropical America. For example, reconstruction of ancestral ecological niches in plants, such as fresh- and saltwater tolerance, might help unravel the underlying landscape in western Amazonia during the Miocene. Also, analyses on the evolution of ecological and physiological traits and their correlations with shifts in diversification rates throughout a phylogenetic tree could improve our understanding of trait selection during lineage divergence. Analyses at lower taxonomic levels (i.e. species complex or a small lineage) and of entire tropical plant communities, using a wealth of approaches including macroecological, phylogenetic and biogeographic, will provide a more thorough understanding of species diversification and distribution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Reconstruction of geographical range evolution inferred by a null model of equal dispersal probabilities across areas in Lagrange.