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Iriarteeae palms tracked the uplift of Andean Cordilleras

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Abstract

Aim: The high biodiversity of northern South America is unparalleled and includes several centres of diversity such as Amazonia, the Andes and the Chocó. Movement of lineages amongst and within these bioregions is thought to be rare, and the effect of those dispersals on the distribution, diversity, and community assembly remains poorly understood. Here we address these effects by studying divergence times, biogeographical history, and species diversification of the palm tribe Iriarteeae, an ecologically dominant forest component.

Location: Central and South America.

Methods: We developed a calibrated phylogeny and a spatially explicit diversification model that incorporates molecular and fossil data. In these analyses, we included a new fossil *Iriartea* species *Gemmamoncolpites galeanoana*, derived from new samples of Miocene deposits in western Amazonia. We also estimated the geographical range evolution of lineages and tested whether speciation and extinction rates were affected by dispersal events using a simulation approach in ClaSSE.

Results: Dispersal amongst bioregions was not evenly distributed across the topology. We found that Amazonian communities are overdispersed across the phylogeny, whereas Andean taxa are clustered. Dispersal events were associated with increases in species diversification and were concomitant with periods of Andean uplift. Migration into montane areas occurred several times from lowland Amazonian ancestors, and montane taxa subsequently recolonized the Amazonian bioregion.

Main conclusions: Our results suggest that the diversification of Iriarteeae palms closely followed the west-to-east surface uplift history of the Northern Andes. From an early, lowland Amazonian ancestor, the first diversification events took place in the earliest emerging mountain chain, the Western Cordillera. From there multiple range expansions followed eastwards and back into the lowlands. This study demonstrates how geological events within a single mountain range can affect the geographical expansion and diversification of lineages.

KEYWORDS

Arecaceae, biogeography, diversification, mountains, Palmae, South America

1 | INTRODUCTION

Northern South America is recognized for its extremely high biodiversity and heterogeneity of habitats (Hoorn et al., 2010). The area spans some of the wettest forests in the world, as well as montane forests along the Andean mountains, the savannas of Los Llanos, the lowlands of the Amazon Basin and some of the oldest terrains on earth, the Brazilian and Guianan Shields (Harrington, 1962). The tropical Andes are a biodiversity hotspot, having the highest rates of endemism and species richness of plants and vertebrates on Earth (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). The Andes constitute a prominent feature of the South American continent, and understanding its geological history is therefore key to understanding its biodiversity.

The Andes have played a fundamental role in species diversification as their uplift created opportunity for allopatric speciation, increased habitat heterogeneity and profoundly changed the environmental conditions of surrounding areas (Antonelli, Nylander, Persson, & Sanmartin, 2009; Luebert & Weigend, 2014). Furthermore, the rise of the Andes had great impact on the formation and retraction of the Miocene Pebas mega-wetland system (Wesselingh, Guerrero, Rasanen, Romero Pitmann, & Vonhif, 2006), which likely covered large expanses of western Amazonia during some periods (Hoorn et al., 2010; Jaramillo et al., 2017). Using species that are restricted to particular biogeographical regions, or simply bioregions (distinct geographical units defined by the evolutionary history and taxonomic composition of their components; see Vilhena & Antonelli, 2015) within northern South America, the temporal evolution of geological formations and biological lineages can be linked to further understand the interplay between landscape changes and biodiversity (Bacon, 2013; Bacon et al., 2015a,b; Hoorn, Mosbrugger, Mulch, & Antonelli, 2013; Jahner et al., 2017; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016).

Few plant clades better characterize both the Andean mountain as well as the lowland Amazonian flora than the palms (Arecaceae; Gentry, 1982). The palm tribe Iriarteae includes Amazonian species, such as *Iriartea deltoidea* and *Socratea exorrhiza*, both of which are recognized as keystone species because of their importance in ecosystem functioning and the sheer number of biotic interactions documented (Galeano & Bernal, 2010) and as some of the most abundant species (hyperdominant; ter Steege et al., 2013). Iriarteae species are also distributed in the mega-diverse Chocó forests of Colombia, Ecuador and Panama, as well as in several of the Andean Cordilleras (Bacon et al., 2016; Henderson, 1990; Restrepo Correa, Núñez Avellaneda, González-Caro, Velásquez-Puentes, & Bacon, 2016). In contrast to some range-restricted species, *Iriartea deltoidea* has an extremely large distribution, predominantly at low and middle elevations (with an upper limit of 1,300 m). It occurs in premontane forests, on steep Andean slopes, down to lowland rainforests, often along stream margins and in successional forest on floodplains (Henderson, 1990; Losos, 1995). Based on a review of 13 Holocene pollen records, Bush and McMichael (2016) demonstrated that *Iriartea*

became hyperdominant in the late Holocene, following increased moisture availability.

Palm fossil flowers have been reported from Iriarteae (late Oligocene to early Miocene; *Socratea*; Poinar, 2002), as well as leaves and fossilized endocarps from Peruvian Miocene (Berry, 1916) and Venezuelan Tertiary (Berry, 1921a,b) deposits, but generic affinities remain elusive. In pre-Quaternary palynological records, *Iriarteae*-type pollen is known from Cretaceous to Palaeogene lowland deposits from an area that is currently formed by the Eastern Cordillera (both Cretaceous–Palaeocene; e.g. Sarmiento, 1992; Van der Hammen & García, 1966) and also in Eocene deposits of the Colombian Llanos (González Guzmán, 1967; Henderson, 1990). New findings of *Iriarteae*-type fossil pollen from western Amazonia and reports from the Neogene record of Panama (Jaramillo et al., 2014) together with a recent phylogeny of the tribe (Bacon et al., 2016), form a robust framework for divergence time estimation and biogeographical inferences. This data availability, combined with the wide distribution across most of northern South America, makes the clade an ideal model for investigating the occurrence and consequences of dispersal events through time and across different Andean Cordilleras and bioregions.

Here, we reconstruct the biogeographical history of Iriarteae palms using both the fossil record and ancestral area analysis. We then estimate the impact of dispersals across different bioregions on species diversification. Overall, we expect (1) few dispersals that, in turn, will cause higher phylogenetic overdispersal in bioregions that have acted primarily as source rather than sink areas, and that (2) these few dispersals will be associated with significant changes in diversification rates. Further, we expect that (3) dispersals across bioregions will correspond to geological time periods with significant mountain uplift from at least 10 Ma and forest expansion after the western Amazonian mega-wetland retreated in the late Miocene. Due to these Cenozoic geological changes in South America, high levels of niche conservatism in palms (Kissling et al., 2012), and the previously documented rarity of biome shifts (Crisp et al., 2009), we expect Iriarteae palm distributions to be affected by geological changes and species to co-vary with dispersals across bioregions.

2 | MATERIALS AND METHODS

2.1 | Study area

Iriarteae palms are conspicuous and abundant across northern South America and adjacent Central America (Henderson, Galeano, & Bernal, 1995). The environmental and physical configuration of this region was greatly affected by its geological history, including the Andean orogeny and its impact on the surrounding landscape and hydrology. The tropical Andes extend from Bolivia north to Colombia and Venezuela. The central and northern ranges are divided by the Amotape–Huancabamba depression in northern Peru that is formed by the Marañón River (Cediel, Shaw, & Caceres, 2003; Graham, Gregory-Wodzicki, & Wright, 2001; Gregory-Wodzicki, 2000). The central Andes rose to their current elevation earlier (10–8 Ma) than the



northern extent (6–4 Ma), and uplift still continues in regions of the Eastern Cordillera of Colombia and the Coastal Cordillera of Venezuela (Bermudez et al., 2015; Hoorn et al., 2010; Mora et al., 2008). Andean orogeny in the Western Cordillera of Colombia and northern Ecuador, together with the emergence of the Panama microplate from under the Pacific Ocean, formed the Chocó region c. 5 Ma (Duque-Caro, 1990a,b). The age of the onset of uplift is largely unknown for the Western Cordillera because it was formed by a mixture of allochthonous terrain that collided with the South American plate, but has generally been attributed to the middle Miocene (Montes et al., 2015). Few data exist for the Central Cordillera, although positive topographic relief has likely been present since the early Cretaceous (Villagomez & Spikings, 2013). Some segments have had positive relief since the Palaeocene (Bayona et al., 2013), while there are two significant pulses of exhumation at 41 and 25–22 Ma for the northern Central Andes (Restrepo-Moreno, Foster, Stockli, & Parra-Sanchez, 2009). Substantial surface uplift (>3 km) has been reported since 15 Ma in the southern Western/Central Cordillera (Pardo-Trujillo et al., 2015; Villagomez & Spikings, 2013). Most of the Eastern Cordillera has had a positive relief since c. 22 Ma (Horton et al., 2010; Ochoa et al., 2012). The palynological record in the Eastern Cordillera shows that most of the modern elevation was reached by 4 Ma (Torres, Vandenberghe, & Hooghiemstra, 2005; Van der Hammen, Werner, & Dommelen, 1973), but new data suggest the high Andes vegetation to have been present between 9.5 and 5.4 Ma (Hoorn et al., 2017). Although many details of the timing and sequence of Andean orogeny are lacking, the evidence presented thus far provides a suitable context for species diversification in the region.

2.2 | Palynological sampling sites

A geological and palynological study was conducted in western Amazonia along the Amazon River at Los Chorros, Puerto Nariño (Colombia) to better understand palaeoenvironmental conditions in Amazonia (Figure 1; Hoorn, 1994). This study also helped to estimate the middle Miocene age based on the presence of markers typical of biostratigraphic zone T15 (14.2–12.7 Ma; Jaramillo, Rueda, & Torres, 2011), as well as led to the discovery of new fossil pollen types. Here new collections were made from these organic-rich clay layers in the Pebas formation and were compared with extant palm taxa using Nomarski differential interference contrast (Bercovici, Hadley, & Villaneuva-Amadoz, 2009).

2.3 | Divergence time estimation

We estimated divergence times based on data from Bacon et al. (2016) but reduced the alignment to one randomly chosen individual per species and including outgroup taxa representing major palm clades to facilitate the dating (*Aphandra natalia*, *Astrocaryum murumuru*, *Chamaedorea tepejilote*, *Geonoma undata*, *Hyospathe macrorhachis*, *Mauritia flexuosa*, *Nypa fruticans*, *Serenoa repens*). The data were partitioned by locus, except for the chloroplast genes that were treated as a

single partition due to inherent linkage, in BEAST 1.8.1 (Drummond, Ho, Phillips, & Rambaut, 2006). The analysis used an uncorrelated lognormal molecular clock model, a Yule pure birth speciation model with a random tree, the GTR+ Γ model of nucleotide substitution with four rate categories, and other prior settings by default. Markov chains were run for 100 million generations and repeated three times. Convergence was verified with effective sample sizes exceeding 200. Half of the trees generated were removed as burn-in and runs were combined in LogCombiner 1.8.1. Mean node heights and 95% highest posterior densities (HPD) were generated in TreeAnnotator 1.8.1.

The analysis was dated based on three fossils, each described by an exponential age prior. *Sabalites carolinensis* (Berry, 1914) is the oldest palm fossil identified to modern affinity, and we placed it as a constraint at the root of the tree. The offset value of the exponential prior was set at 85.8 Ma and the mean at 1.00 to fully represent the fossil age range (Harley, 2006). The amber-preserved flowers of *Socratea brownii* (Poinar, 2002) have open, sessile, staminate flowers with 20 and 100 stamens, all diagnostic characters of the genus *Socratea*. We placed this constraint on the crown node of *Socratea* with an offset value of the exponential prior set to 22.5 Ma and the standard deviation at 1.17 Ma. The third calibration was placed on the crown node of *Iriarteia*, based on the here-reported fossil pollen and the age of the deposit, with an offset of 11.6 Ma and a standard deviation of 1.4. Subsequently, all macroevolutionary analyses used the maximum clade credibility tree with outgroups pruned.

2.4 | Geographical evolution of Iriarteae

We estimated range evolution in BioGeoBEARS (Matzke, 2013), under the dispersal–extinction–cladogenesis model (DEC; Ree & Smith, 2008). This and all subsequent analyses were conducted in R (R Core Team, 2014). We implemented an unconstrained analysis defining bioregions as follows: A—Lowland Amazonia (<500 m in elevation; comprising parts of Brazil, Colombia, Ecuador, Peru), B—Western Andean Cordillera (above 500 m; Ecuador and Colombia), C—Central Andean Cordillera Andes (above 500 m; Colombia), D—Eastern Andean Cordillera (above 500 m; Colombia and Venezuela), E—Chocó (below 500 m, Colombia, Ecuador, Panama). The use of the threshold of 500-m elevation was chosen based on the classification of palm diversity by Galeano and Bernal (2010), who demonstrated this to represent a natural elevational divide for many taxa.

2.5 | Phylogenetic community structure

To understand community assembly across bioregions, and its relation to the biogeographical history of clades, we measured the degree of phylogenetic structure within and among the three major bioregions of the current distribution of Iriarteae (Amazonia, Andes, and Chocó; Figure S1 in Appendix S1). We used the standardized effects of the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) indexes that are related to the net relatedness index and nearest taxon index (Webb, Ackerley, McPeck, & Donoghue, 2002). These metrics compare the observed value of the

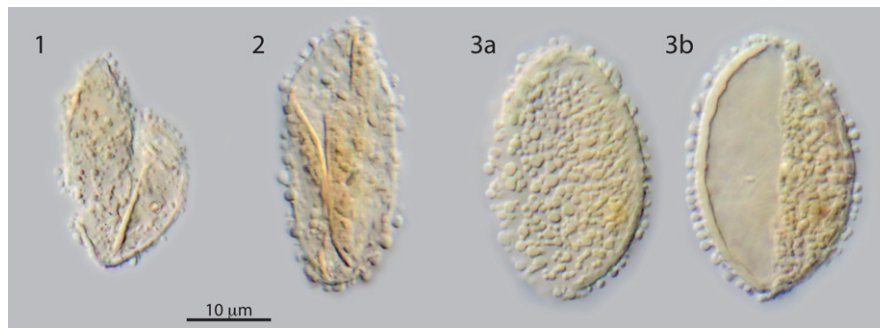


FIGURE 1 Pollen microphotography and plate composition for *Gemmamonocolpites galeanoana* (1 and 2) and *Iriartea deltoidea* (3a and b). Fossil pollen of *G. galeanoana* was discovered in Miocene deposits along the Amazon River at Los Chorros, Puerto Nariño (Colombia)

MPD and MNTD with values generated under a null model, formulated by reshuffling taxa on the topology over 1,000,000 iterations, using PICANTE 1.5-2 (Kembel et al., 2010). Resulting values near zero indicate phylogenetically random assemblages and values greater than zero indicate phylogenetic clustering, while values below zero indicate overdispersion (Webb et al., 2002).

Additionally, we measured the degree of phylogenetic turnover among bioregions using the PI_{ST} index implemented in SPACODIR 0.13.0115 (Eastman, Paine, & Hardy, 2011). The PI_{ST} index compares the degree of relatedness among communities containing different species. We established the significance of our estimations by generating a null distribution of PI_{ST} values by reshuffling taxa across the topology 100,000 times and comparing the observed values with the null distribution.

2.6 | Bioregion-specific diversification rates

To estimate speciation, extinction and dispersal rates associated with the three major bioregions we extended the GeoSSE model to three states (Goldberg, Lancaster, & Ree, 2011) in ClaSSE, implemented in diversitree 0.9-3 (Fitzjohn, 2012). ClaSSE allows for models with more than two geographical areas or traits by applying constraints to a full model allowing for all possible dispersal, speciation and extinction parameters for a given number of states.

We defined the same parameters as in the GeoSSE model extended to include the three bioregions: Amazonia, Andes and Chocó (Figure S1 in Appendix S1). As some species are currently present in two areas, but never three, we reduced model complexity by prohibiting three area states. Our ClaSSE model had 6 states and 13 parameters that were subjected to further constraints (Table 1): (1) the speciation within bioregion parameter was constrained to speciation events occurring within the range from a single or widespread parental lineage, as in the GeoSSE model; (2) the speciation-between-bioregion parameters were constrained into single parameter representing an overall speciation-by-bioregion divergence rate; (3) the range transition parameters were constrained to occur in single steps. To require range expansion and/or contraction events to be effective we imposed three constraints: first, that state changes between two single-ranged states were not allowed; second, that

state transitions between widespread and single ranges were restricted when common areas between the involved states were absent; third, that transitions between two widespread ranges could not occur directly, nor could a two-ranged lineage go extinct without reducing its distribution first to a single range, as in the GeoSSE model.

We used a maximum likelihood approach to simulate diversification and dispersal parameters associated with bioregions using 1,000 dated phylogenies from the posterior Bayesian sample. In order to test the reliability of our method, trees were simulated under known parameter values and analysed under our three-geographic area model using a maximum likelihood approach. A total of 2,500 simulated birth-death trees were generated using the function “trees” in diversitree. We used this function to define a ClaSSE-type model with the 13 parameters defined by our model, resulting in trees with 30 terminals, each with a given state (A, B, C, AB, BC or AC). We then selected 1,000 trees and checked that those had all six states present, as some simulated trees recovered fewer less six states. Finally, we used those 1,000 trees and fit our ClaSSE model using each simulated tree to obtain parameter estimates (Table 2).

3 | RESULTS

3.1 | Fossil pollen of *Iriartea* and extant affinity in Amazonia

Pollen and spores are abundant in the Pebas formation, and composed of taxa typical of a wetland environment, including the extinct palm *Grimsdalea* as well as *Iriartea*. The sediments are identified as containing fossils from the local vegetation combined with pollen that eroded from the montane Andean forest (Hoorn, 1993). We discovered three grains that have affinity to *Iriartea*, two of which are described here and are assigned to the new species *Gemmamonocolpites galeanoana* Hoorn and Bacon (Appendix S2). The third grain is not informative enough to allow a precise identification, but given its overall similarity to other species in the genus we treat it as *Gemmamonocolpites* sp. All the pollen morphological features and measurements together with the comparison with extinct and modern *Iriartea*, are listed in Table S1 in Appendix S1.

TABLE 1 Parameters and constraints used in our three-area model. Numbers indicate the states (bioregions) used: AB (1), AC (2), A (3), B (4), C (5), BC (6), where A is Amazonia, B is the Andes and C is the Chocó. λ refers to speciation events (followed by three numbers, the first one indicating the parental species state followed by two other numbers indicating the states of the resulting daughter lineages), q refers to range expansion or range contraction events (followed by two numbers indicating state change—i.e. expansion or contraction—from one state to another) and μ refers to extinction events (followed by the number of states subject to extinction)

Speciation within bioregions	Speciation between bioregions	Extinction/Range contraction	Range expansion
$s A = \lambda_{333} = \lambda_{113} = \lambda_{223}$	$s \text{ Bet} = \lambda_{134} = \lambda_{235} = \lambda_{645}$	$x A = \mu_{33} = q_{14} = q_{25}$	$d (A-AB) = q_{31}$
$s B = \lambda_{444} = \lambda_{114} = \lambda_{646}$		$x B = \mu_{44} = q_{13} = q_{65}$	$d (B-AB) = q_{41}$
$s C = \lambda_{555} = \lambda_{225} = \lambda_{656}$		$x C = \mu_{55} = q_{23} = q_{64}$	$d (C-AC) = q_{52}$
			$d (A-AC) = q_{32}$
			$d (B-BC) = q_{46}$
			$d (C-BC) = q_{56}$

TABLE 2 Comparison of the estimated (median values across trees) and the simulated data under the three-bioregion model (A is Amazonia, B is the Andes, and C is the Chocó), where speciation, extinction and dispersal are abbreviated s , x and d respectively. Speciation between bioregions is shown by $s \text{ Bet}$

Parameter	Real value	Median	% Difference	5%–95% Quantiles
$s A$	1.2	1.07	10.83	0, 2.98
$s B$	1.8	1.69	6.11	0.62, 3.63
$s C$	0.9	0.81	10	0, 2.69
$s \text{ Bet}$	0.6	0.44	26.66	0, 2.98
$x A$	0.7	0	100	0, 4.62
$x B$	0.8	0.49	26.25	0, 4.58
$x C$	0.5	0	100	0, 5.37
$d (A-AB)$	1.2	0.95	20.83	0, 7.5
$d (B-BC)$	0.8	0.8	0	0, 3.58
$d (C-AC)$	1.8	1.37	23.88	0, 11.03
$d (B-AB)$	0.5	0.47	6	0, 3.45
$d (C-BC)$	1.5	1.12	25.33	0, 11.44
$d (A-AC)$	1	1.2	20	0, 8.49

3.2 | Divergence times and range evolution

The phylogeny resolved inter-generic and interspecific relationships with overall high posterior probabilities (Figure 2) and were consistent with previous work (Bacon et al., 2016). The crown node of the tribe was inferred during the Eocene (mean age 43 Ma; 56.9–31.4 Ma) and the ancestral range was largely ambiguous. The ancestral range of *Iriarteae*+*Dictyocaryum* was probably widespread across northern South America during the Miocene, whereas the ancestor of the remainder of the tribe was much older (Eocene; mean age of 39 Ma) and most likely distributed in Amazonia (area A; Figure 2). Ancestral lineages of *Wettinia*+*Socratea* were primarily distributed in Amazonia and the Western Cordillera of the Colombian Andes (areas A and B) in the late Eocene (mean age of 35 Ma), and although the ancestral distribution of *Socratea* is largely ambiguous, the Western Cordillera continued to be fundamental for the diversification of *Wettinia*, particularly in the Miocene as shown by the area

reconstructions (Figure 2). Only more recently did the Central and Eastern Cordilleras of Colombia become colonized, in the late Miocene and late Pliocene respectively. This pattern is particularly evident and strongly supported in *Wettinia*, where a vicariance event is inferred in the Central and Eastern Cordilleras and *W. anomala* was distributed in the Central Cordillera and the ancestor of *W. microcarpa* and *W. praemorsa* dispersed into the Eastern Cordillera <3 Ma. From an ancestral Amazonian range, the genus *Wettinia* underwent diversification in the Andes during the Miocene, then recolonized Amazonia c. 5 Ma, resulting in two species endemic to the bioregion.

3.3 | Community assembly and diversification in Iriarteae

Phylogenetic structure and general patterns of phylogenetic diversity, as inferred from the MPD metric, showed two statistically significant results (Table S2 in Appendix S1) where Amazonian species are phylogenetically overdispersed and the Andean lineages are clustered. When considering phylogenetic turnover, the beta diversity between the Amazonian and Andean communities differed significantly ($PI_{ST} \sim 0.06$; Figure S2 in Appendix S1).

In the ClaSSE analysis we found that our model based on the 13 parameters is highly recoverable from simulated data, showing that species diversification was strongly determined by bioregion occurrence (Figure S3 in Appendix S1). Although posterior distributions of dispersal, extinction and speciation as inferred from our model in *Iriarteae* were largely overlapping, median values suggest that speciation and extinction are higher in the Andean bioregion compared to the two others (Figure S4 in Appendix S1). Further, dispersal from Chocó to Amazonia and from Amazonia to the Andes had the highest rates of all combinations of dispersal.

4 | DISCUSSION

We inferred the evolutionary history of *Iriarteae* palms and examined bioregion-driven diversification, combining ancestral range estimation on a dated phylogenetic tree integrated with the fossil

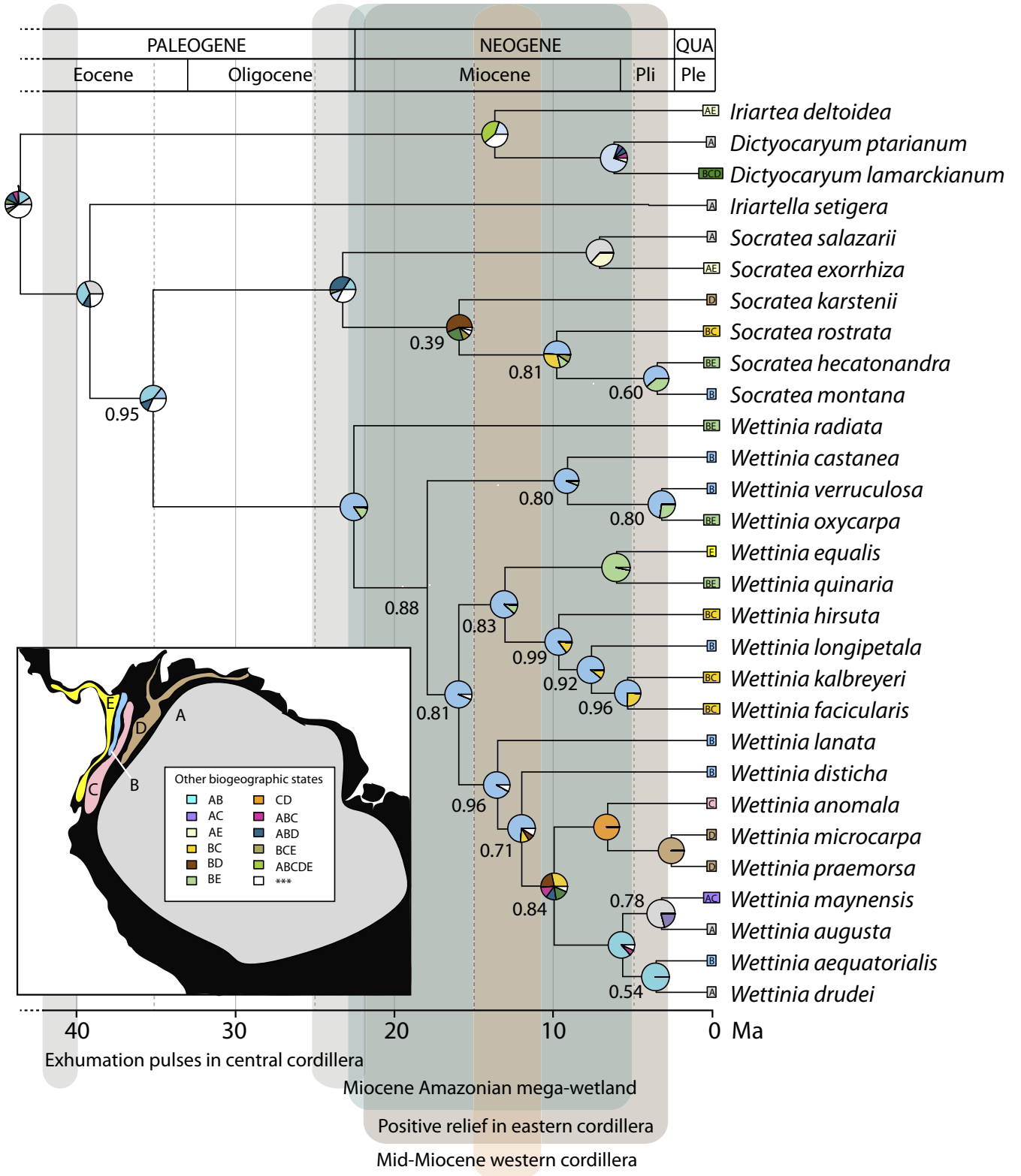


FIGURE 2 Dated molecular phylogeny of the palm tribe Iriarteae based on 11 genes and node calibrated with three fossils. Ancestral range reconstruction using five areas (inset) and extant distributions (coloured squares at tips) is shown as pie charts at nodes. White sections of the pie charts represent all combined distributions with a probability of <0.05 inferred for that node. Branch support values lower than 1.0 posterior probability are shown below nodes. Major landscape changes through time are coloured along the chronogram: exhumation pulses in the Central Cordillera (Pardo-Trujillo et al., 2015; Restrepo-Moreno et al., 2009; Villagomez & Spikings, 2013), Miocene Amazonian mega-wetland (Hoorn et al., 2010; Jaramillo et al., 2017), positive relief in the Eastern cordillera (Horton et al., 2010; Ochoa et al., 2012), and mid-Miocene Western Cordillera (Montes et al., 2015)



record. The temporal framework of this study is consistent with previous studies (Baker & Couvreur, 2013; Couvreur, Forest, & Baker, 2011), where our results fall within previous credibility intervals. We expected and found evidence for relatively few dispersals between Amazonia, Andes and Chocó bioregion. Dispersals were associated with uplift of the Andes and the presence of the Miocene Pebas mega-wetland affecting lowland sites, where dispersal events were associated with changes in diversification rates.

4.1 | Range evolution

The study of our new fossil discoveries shows that *Gemmamonocolpites barbatus* (Eocene) strongly resembles *Iriarte* and *G. galeanoana* (Miocene). This affinity suggests that *Iriarte* ancestors have a long history, deeply rooted in the Cenozoic (63 Ma mean stem age of the tribe). Both the Eocene and Miocene deposits in which *G. barbatus* and *G. galeanoana* were formed are indicative of lowland, estuarine conditions. The deposition scenario of these pollen grains further suggests that ancestral lowland lineages were affected by the Miocene mega-wetland in western Amazonia. *Iriarte* is a monotypic genus today but it could have lost diversity during climatic and habitat changes as a result of marine incursions in Amazonia (Jaramillo et al., 2017). Diversification and population structure have also been shown to be influenced by these wetlands in *Astrocaryum* palms (Roncal, Kahn, Millan, Couvreur, & Pintaud, 2013; Roncal et al., 2015). Furthermore, the results from the ancestral area analysis show that vicariance was an important factor affecting distributions (Figure 2). As the Andes mountains rose, they split former large distributions, such as *Iriarte deltoidea* and *Socratea exorrhiza*, which are abundant in the lowlands of both Amazonia and Chocó.

From the Palaeogene onwards, lowland Iriarteeae lineages diversified concomitantly with the Andean uplift, with the Western Cordillera of Colombia playing a key role for diversification (Figure 2). Few studies have included fine-scale sampling across the northern Andean cordilleras, but a recent study showed the Western Cordillera as being the ancestral distribution for butterflies (De-Silva, Elias, Willmott, Mallet, & Day, 2016), although at more recent time-scales than for Iriarteeae. Furthermore, reduced differentiation between montane species inhabiting the Central and Western Cordilleras of Colombia suggest connectivity and/or recent divergence (Chaves & Smith, 2011). The geological evolution of the Western Cordillera is still debated, but its ancient origins and increased exhumation rates from 15 Ma (Pardo-Trujillo et al., 2015; Villagomez & Spikings, 2013) are both corroborated by the results of the calibrated phylogeny, where the Western Cordillera is colonized in the early Cenozoic and reconstructed as the ancestral distribution for many lineages in the Miocene (Figure 2). The Central and Eastern Cordilleras are subsequently colonized in the middle to late Miocene (Figure 2). Geological evidence for the timing of these terrains is an active area of research, yet a late Miocene elevation gain has been proposed (Anderson, Saylor, Shanahan, & Horton, 2015; Torres et al., 2005; Van der Hammen et al., 1973) and is consistent with our biogeographical results. The inference of ancestral ranges in the Chocó

(ca. 15–7 Ma; Figure 2) are also consistent with geological information that eludes to the formation of Chocó-like conditions (e.g. orographic precipitations, hyperpluvial system, major fluvial networks, high biodiversity, reduction in sea surface salinity) starting c. 16 Ma with sustained activity until c. 5 Ma (Pardo-Trujillo et al., 2015). We find corroboration of distributions and diversification in palm clades in relation to the geological history of the Andes (*Aiphanes*, Eiserhardt et al., 2011; Iriarteeae, here; *Ceroxylon*, Sanin et al., 2016; *Cryosophila*, Cano et al., 2018), showing palms tracked these highly dynamic geological systems.

4.2 | Bioregion evolution

When the geographical distribution of Iriarteeae is split into three major bioregions (Amazonia, the Andes and the Chocó), we find species turnover to be significant between the Andes and Amazonia, complemented by significant phylogenetic structure of these bioregions (Table S2 in Appendix S1). The ClaSSE analysis showed that both speciation and extinction rates are higher in the Andes than in the other bioregions. Furthermore, the dispersal rate from Amazonia to the Andes was the highest of all possible combinations. The Chocó did not recover significant results for either species turnover or phylogenetic community structure, although the bioregion recovered one of the highest rates of overall dispersal from the bioregion-driven diversification rate tests. Taken together, these results on the Chocó may be explained by the fact that the bioregion harbours a lower number of species that are concentrated in two clades of *Wettinia*, and any biogeographical pattern may be masked by its potentially shared history with the lowlands of Amazonia and strong connections with Central America that were not accounted for in this study. Although issues with small phylogenies and the performance of SSE suite of methods have been identified (Davis, Midford, & Maddison, 2013; Gamisch, 2016), we show with simulations that the parameter values of the model of empirical range evolution in Iriarteeae are highly recoverable in our ClaSSE analysis (Figure S4).

Recent studies increasingly show that phylogenetic conservatism is not a general rule, such as in the Neotropics (Antonelli & Sanmartín, 2011), or at finer spatial scales (Donoghue & Edwards, 2014). For example, the Cerrado bioregion has been shown to be a sink for various lineages in both neighbouring and distant bioregions, such as rainforests, seasonally dry forests, subtropical grasslands and wetlands, where shifts drove morphological adaptations to fire resistance (Bacon, Moraes, Jaramillo, & Antonelli, 2017; Simon et al., 2009). At finer scales, Souza-Neto, Cianciaruso, and Collevatti (2016) show that habitat shifts and dispersal are an important part of Cerrado legume diversity. Our results also show multiple migration events amongst bioregions, in particular between Amazonia and the Andes.

It has been suggested that habitat heterogeneity and complex topography have created Andean diversity, rather than orogeny (Mutke, Jacobs, Meyers, Henning, & Weigend, 2014), but this is an incorrect dichotomy when considering that habitat diversification and changes in topography are a direct result of mountain building

and associated climate changes. Most published results in vertebrates point to lowland origins for a majority of clades (e.g. Brumfield & Edwards, 2007), which is consistent with the Amazonian origin for Iriarteeae palms. In contrast, a study of dendrobatid frogs (Santos et al., 2009) showed that a majority of dispersals occurred from the Andes into Amazonia. As pointed out by Brumfield and Edwards (2007), pinpointing vicariant events that played a role in the isolation of colonizing Andean populations from source lowlands populations is difficult because of the long and dynamic history of the bioregion in combination with climatic fluctuations (e.g., Gosling & Bush, 2005). This is also a general concern in biogeographic studies, where geological and climatic events are often inter-linked and it may be difficult to propose causation rather than correlation (Linder, Rabosky, Antonelli, Wüest, & Ohlemüller, 2014). Many idiosyncrasies of Andean radiations remain to be fully understood, including the role of biogeographical history. Even after over 200 years of work dedicated to the understanding of the intimate relationships between the Andes and their fantastic diversity (von Humboldt & Bonpland, 1807), we continue to make interesting discoveries.

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REFERENCES

- Anderson, V. J., Saylor, J. E., Shanahan, T. M., & Horton, B. K. (2015). Paleoelevation records from lipid biomarkers: Application to the tropical Andes. *Geological Society of America Bulletin*, 127, 1604–1616. <https://doi.org/10.1130/B31105.1>
- Antonelli, A., Nylander, J. A. A., Persson, C., & Sanmartín, I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences, USA*, 106, 9749–9754. <https://doi.org/10.1073/pnas.0811421106>
- Antonelli, A., & Sanmartín, I. (2011). Why are there so many plant species in the Neotropics? *Taxon*, 60, 403–414.
- Bacon, C. D. (2013). Biome evolution and biogeographical change through time. *Frontiers in Biogeography*, 5, e4.
- Bacon, C. D., Moraes, M., Jaramillo, C., & Antonelli, A. (2017). Endemic palm species shed light on habitat shifts and the assembly of the Cerado and Restinga floras. *Molecular Phylogenetics and Evolution*, 110, 127–133. <https://doi.org/10.1016/j.ympev.2017.03.013>
- Bacon, C. D., Silvestro, D., Jaramillo, C. A., Smith, B. T., Chakrabarty, P., & Antonelli, A. (2015a). Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proceedings of the National Academy of Sciences*, 112, 6110–6115. <https://doi.org/10.1073/pnas.1423853112>
- Bacon, C. D., Silvestro, D., Jaramillo, C. A., Smith, B. T., Chakrabarty, P., & Antonelli, A. (2015b). Reply to Lessios and Marko et al.: Early and progressive migration across the Isthmus of Panama is robust to missing data and biases. *Proceedings of the National Academy of Sciences*, 112, e5767–e5768. <https://doi.org/10.1073/pnas.1515451112>
- Bacon, C. D., Velasquez-Puentes, F., Florez-Rodriguez, A., Balslev, H., Galeano, G., Bernal, R., & Antonelli, A. (2016). Phylogenetics of Iriarteeae (Arecaceae), cross-Andean disjunctions and convergence of clustered infructescence morphology in *Wettinia*. *Botanical Journal of the Linnean Society*, 182, 272–286. <https://doi.org/10.1111/boj.12421>
- Baker, W. J., & Couvreur, T. L. P. (2013). Global biogeography and diversification of palms sheds lights on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography*, 40, 274–285.
- Bayona, G., Cardona, A., Jaramillo, C., Mora, A., Montes, C., Caballero, V., ... Inbanaz, M. (2013). Onset of fault reactivation in the Eastern Cordillera of Colombia and proximal Llanos basin; response to Caribbean - South American collision in early Palaeogene time. In M. Nemcock, A. Mora, & J. W. Cosgrove (Eds.), *Thick-skin-dominated orogens: From initial to full accretion* (pp. 285–314). London: Geological Society of London Special Publication.
- Bercovici, A., Hadley, A., & Villaneuva-Amadoz, U. (2009). Improving depth of field resolution for palynological photomicrography. *Palaeontologia Electronica*, 12, 12.
- Bermudez, M. A., Hoorn, C., Bernet, M., Carrillo, E., van der Beek, P. A., Garver, J. I., ... Mehrkian, K. (2015). The detrital record of Late-Miocene to Pliocene surface uplift and exhumation of the Venezuelan Andes in the Maracaibo and Barinas foreland basins. *Basin Research*, 29, 370–395.
- Berry, E. W. (1914). The Upper Cretaceous and Eocene floras of south California and Georgia. *United States Geological Survey*, 84, 1–200.
- Berry, E. W. (1916). Lower Eocene floras of southeastern North America. *U.S. Geological Survey Professional Paper*, 91, 1–481.
- Berry, E. W. (1921a). Tertiary fossil plants from Venezuela. *Proceedings of the United States National Museum*, 59, 553–579. <https://doi.org/10.5479/si.00963801.59-2388.553>
- Berry, E. W. (1921b). A palm nut from the Miocene of the Canal Zone. *Proceedings of the United States National Museum*, 59, 21–22. <https://doi.org/10.5479/si.00963801.59-2356.21>
- Brumfield, R. T., & Edwards, S. V. (2007). Evolution into and out of the Andes: A Bayesian analysis of historical diversification in *Thamnopilius* antshrikes. *Evolution*, 61, 346–367. <https://doi.org/10.1111/j.1558-5646.2007.00039.x>
- Bush, M. B., & McMichael, C. N. H. (2016). Holocene variability of an Amazonian hyperdominant. *Journal of Ecology*, 104, 1370–1378. <https://doi.org/10.1111/1365-2745.12600>
- Cano, Á., Bacon, C. D., Stauffer, F. W., Antonelli, A., Serrano-Serrano, M. L., & Perret, M. (2018). The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. *Journal of Biogeography*. <https://doi.org/10.1111/jbi.13225>



- Cediel, F., Shaw, R. P., & Caceres, C. (2003). Tectonic assembly of the Northern Andean Block. In C. Bartolini, R. T. Buffler, & J. Blickwede (Eds.), *The circum-gula of Mexico and the Caribbean habitats, basin formation, and plate tectonics*. AAPG Memoir 79, 815–848.
- Chaves, J. A., & Smith, T. B. (2011). Evolutionary patterns of diversification in the Andean hummingbird genus *Adelomyia*. *Molecular Phylogenetics and Evolution*, 60, 207–218. <https://doi.org/10.1016/j.ympev.2011.04.007>
- Couvreur, T. L. P., Forest, F., & Baker, W. J. (2011). Origin and global diversification patterns of tropical rain forests: Inferences from a complete genus-level phylogeny of palms. *BMC Biology*, 9, e44. <https://doi.org/10.1186/1741-7007-9-44>
- Crisp, M. D., Arroyo, M. T., Cook, L. G., Gandolfo, M. A., Jordan, G. J., McGlone, M. S., ... Linder, H. P. (2009). Phylogenetic biome conservatism on a global scale. *Nature*, 458, 754–756. <https://doi.org/10.1038/nature07764>
- Davis, M., Midford, P., & Maddison, W. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology*, 13, e38. <https://doi.org/10.1186/1471-2148-13-38>
- De-Silva, D. L., Elias, M., Willmott, K., Mallet, J., & Day, J. J. (2016). Diversification of clearwing butterflies with the rise of the Andes. *Journal of Biogeography*, 43, 44–58. <https://doi.org/10.1111/jbi.12611>
- Donoghue, M. J., & Edwards, E. J. (2014). Biome shifts and niche evolution in plants. *Annual Review of Ecology, Evolution, and Systematics*, 45, 547–572. <https://doi.org/10.1146/annurev-ecolsys-120213-091905>
- Drummond, A. J., Ho, S. Y., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology*, 4, e88. <https://doi.org/10.1371/journal.pbio.0040088>
- Duque-Caro, H. (1990a). The Choco block in the northwestern corner of South America: Structural, tectonostratigraphic, and paleogeographic implications. *Journal of South American Earth Sciences*, 3, 71–84. [https://doi.org/10.1016/0895-9811\(90\)90019-W](https://doi.org/10.1016/0895-9811(90)90019-W)
- Duque-Caro, H. (1990b). Neogene stratigraphy, paleoceanography and paleobiogeography in northwest South America and the evolution of the Panama Seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 77, 203–234. [https://doi.org/10.1016/0031-0182\(90\)90178-A](https://doi.org/10.1016/0031-0182(90)90178-A)
- Eastman, J. M., Paine, C. E. T., & Hardy, O. J. (2011). spacodiR: Structuring of phylogenetic diversity in ecological communities. *Bioinformatics*, 27, 2437–2438. <https://doi.org/10.1093/bioinformatics/btr403>
- Eiserhardt, W. L., Pintaud, J.-C., Asmussen-Lange, C., Hahn, W. J., Bernal, R., Balslev, H., & Borchsenius, F. (2011). Phylogeny and divergence times of Bactidinae (Arecaceae, Palmae) based on plastid and nuclear DNA sequences. *Taxon*, 60, 485–498.
- Fitzjohn, R. G. (2012). Diversitree: Comparative phylogenetic analysis of diversification in R. *Methods in Ecology and Evolution*, 3, 1084–1092. <https://doi.org/10.1111/j.2041-210X.2012.00234.x>
- Galeano, G., & Bernal, R. (2010). *Palmas de Colombia. Guía de Campo*. Bogota, Colombia: Instituto de Ciencias Naturales, Facultad de Ciencias, Universidad Nacional de Colombia.
- Gamisch, A. (2016). Notes on the statistical power of the binary state speciation and extinction (BiSSE) model. *Evolutionary Bioinformatics*, 12, 165–174.
- Gentry, A. H. (1982). Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, 69, 557–593. <https://doi.org/10.2307/2399084>
- Goldberg, E. E., Lancaster, L. T., & Ree, R. H. (2011). Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology*, 60, 451–465. <https://doi.org/10.1093/sysbio/syr046>
- González Guzmán, A. E. (1967). *A palynological study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene; Tibu area, Colombia)*. Leiden: E. J. Brill.
- Gosling, W. D., & Bush, M. B. (2005). A biogeographic comment on: Wuster et al. (2005) Tracing an invasion: Landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). *Molecular Ecology*, 14, 3615–3617. <https://doi.org/10.1111/j.1365-294X.2005.02642.x>
- Graham, A., Gregory-Wodzicki, K. M., & Wright, K. L. (2001). Studies in Neotropical paleobotany XV. A Mio-Pliocene palynoflora from the Eastern Cordillera, Bolivia: Implications for the uplift history of the Central Andes. *American Journal of Botany*, 88, 1545–1557. <https://doi.org/10.2307/3558398>
- Gregory-Wodzicki, K. M. (2000). Uplift history of the central and northern Andes: A review. *Geological Society of America Bulletin*, 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. *Botanical Journal of the Linnean Society*, 151, 39–67. <https://doi.org/10.1111/j.1095-8339.2006.00522.x>
- Harrington, H. J. (1962). Paleogeographic development of South America. *American Association of Petroleum Geologists Bulletin*, 46, 1–1814.
- Henderson, A. H. (1990). Arecaceae. Part I Introduction and the Iriarteinae. *Flora Neotropica*, 53, 1–100.
- Henderson, A. H., Galeano, G., & Bernal, R. (1995). *Field guide to the Palms of the Americas*. Princeton, NJ: Princeton University Press.
- Hoorn, C. (1993). Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 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). An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 112, 187–238. [https://doi.org/10.1016/0031-0182\(94\)90074-4](https://doi.org/10.1016/0031-0182(94)90074-4)
- Hoorn, C., Bogotá-A, G. R., Romero-Baez, M., Lammertsma, E. I., Flantua, S. G. A., Dantas, E. L., ... Chemale, F. (2017). The Amazon at sea: Onset and stages of the Amazon River from a marine record, with species reference to Neogene plant turnover in the drainage basin. *Global and Planetary Change*, 153, 51–65. <https://doi.org/10.1016/j.gloplacha.2017.02.005>
- Hoorn, C., Mosbrugger, V., Mulch, A., & Antonelli, A. (2013). Biodiversity from mountain building. *Nature Geoscience*, 6, 154. <https://doi.org/10.1038/ngeo1742>
- Hoorn, C., Wesseling, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., ... Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. *Science*, 330, 927–931. <https://doi.org/10.1126/science.1194585>
- Horton, B. K., Parra, M., Saylor, J. E., Nie, J., Mora, A., Torres, V., ... Strecker, M. R. (2010). Resolving uplift of the northern Andes using detrital zircon age signatures. *GSA Today*, 20, 4–9. <https://doi.org/10.1130/GSATG76A.1>
- Jahner, J. P., Forister, M. L., Parchman, T. L., Smilanich, A. M., Miller, J. S., Wilson, J. S., ... Dyer, L. A. (2017). Host conservatism, geography, and elevation in the evolution of a Neotropical moth radiation. *Evolution*, 71, 2885–2900. <https://doi.org/10.1111/evo.13377>
- Jaramillo, C., Moreno, E., Ramírez, V., da Silva, S., de la Barrera, A., de la Barrera, A., ... Hoyos, N. (2014). Palynological record of the last 20 million years in Panama. *A Festschrift for Alan Graham in his 80th year* (pp. 134–251). St Louis, MO, USA: Missouri Botanical Garden Press.
- Jaramillo, C., Romero, I., D'Apollito, C., Bayona, G., Duarte, E., Louwye, S., ... Wesseling, F. P. (2017). Miocene flooding events of western Amazonia. *Science Advances*, 3, e1601693. <https://doi.org/10.1126/sciadv.1601693>

- Jaramillo, C. A., Rueda, M., & Torres, V. (2011). A palynological zonation for the Cenozoic of the Llanos and Llanos Foothills of Colombia. *Palynology*, 35, 46–84. <https://doi.org/10.1080/01916122.2010.515069>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerley, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kissling, W. D., Baker, W. J., Balslev, H., Barford, A. S., Borchsenius, F., Dransfield, J., ... Svenning, J.-C. (2012). Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, 21, 909–921. <https://doi.org/10.1111/j.1466-8238.2011.00728.x>
- 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 Phytologist*, 210, 1430–1442. <https://doi.org/10.1111/nph.13920>
- Linder, H. P., Rabosky, D. L., Antonelli, A., Wüest, R. O., & Ohlemüller, R. (2014). Disentangling the influence of climatic and geological changes on species radiations. *Journal of Biogeography*, 41, 1313–1325. <https://doi.org/10.1111/jbi.12312>
- Losos, E. (1995). Habitat specificity of two palm species: Experimental transplantation in Amazonian successional forests. *Ecology*, 76, 2595–2606. <https://doi.org/10.2307/2265830>
- Luebert, F., & Weigend, M. (2014). Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution*, 2, 1–27.
- Matzke, N. J. (2013). *BioGeography with Bayesian (and Likelihood) evolutionary analysis in R scripts*. Retrieved from <https://cran.r-project.org/web/packages/BioGeoBEARS/BioGeoBEARS.pdf>
- Montes, C., Cardona, A., Jaramillo, C. A., Pardo, A., Silva, J. C., Valencia, V., ... Nino, H. (2015). Middle Miocene closure of the Central American Seaway. *Science*, 348, 226–229. <https://doi.org/10.1126/science.aaa2815>
- Mora, A., Parra, M., Strecker, M. R., Sobel, E. R., Hooghiemstra, H., Torres, V., & Vallejo-Jaramillo, J. (2008). Climatic forcing of asymmetric orogenic evolution in the Eastern Cordillera of Colombia. *The Geological Society of America Bulletin*, 120, 930–949. <https://doi.org/10.1130/B26186.1>
- Mutke, J., Jacobs, R., Meyers, K., Henning, T., & Weigend, M. (2014). Diversity patterns of selected Andean plant groups correspond to topography and habitat dynamics, not orogeny. *Frontiers in Genetics*, 5, e351.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>
- Ochoa, D., Hoorn, C., Jaramillo, C. A., Bayona, G., de la Parra, F., & Parra, M. (2012). The final phase of tropical lowland conditions in the axial zone of the eastern cordillera of Colombia: Evidence from three palynological records. *Journal of South American Earth Sciences*, 39, 157–169. <https://doi.org/10.1016/j.jsames.2012.04.010>
- Pardo-Trujillo, A., Restrepo-Moreno, S. A., Vallejo, D. F., Flores, J. A., Trejos, R. A., & Foster, D. A., ... Kamenov, G. D. (2015). New thermotectonic and paleo-environmental constraints from the western cordillera and associated sedimentary basins (Northern Andes, Colombia): The birth of a major orographic barrier and the Choco biogeographic region? *Geological Society of America*. Baltimore, MD. Retrieved from <https://gsa.confex.com/gsa/2015AM/webprogram/Paper270401.html>
- Poinar, G. (2002). Fossil palm flowers in Dominican and Mexican amber. *Botanical Journal of the Linnean Society*, 138, 57–61.
- R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>.
- Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57, 4–14. <https://doi.org/10.1080/10635150701883881>
- Restrepo Correa, Z., Núñez Avellaneda, L. A., González-Caro, S., Velásquez-Puentes, F., & Bacon, C. D. (2016). Exploring palm - pollinator interaction across geographic and environmental gradients. *Botanical Journal of the Linnean Society*, 182, 389–397. <https://doi.org/10.1111/boj.12443>
- Restrepo-Moreno, S. A., Foster, D. A., Stockli, D. F., & Parra-Sanchez, L. N. (2009). Long-term erosion and exhumation of the “Altiplano Antioqueño”, Northern Andes (Colombia) from apatite (U–Th)/He thermochronology. *Earth and Planetary Science Letters*, 278, 1–12. <https://doi.org/10.1016/j.epsl.2008.09.037>
- Roncal, J., Couderc, M., Baby, P., Kahn, F., Millán, B., Meerow, A. W., & Pintaud, J.-C. (2015). Palm diversification in two geologically contrasting regions of western Amazonia. *Journal of Biogeography*, 42, 1503–1513. <https://doi.org/10.1111/jbi.12518>
- Roncal, J., Kahn, F., Millan, B., Couvreur, T. L. P., & Pintaud, J.-C. (2013). Cenozoic colonization and diversification patterns of tropical American palms: Evidence from *Astrocaryum* (Arecaceae). *Botanical Journal of the Linnean Society*, 171, 120–139. <https://doi.org/10.1111/j.1095-8339.2012.01297.x>
- Sanin, M. J., Kissling, W. D., Bacon, C. D., Borchsenius, F., Galeano, G., Svenning, J.-C., ... Pintaud, J.-C. (2016). The Neogene rise of the Northern Andes triggered species diversification through geographic colonization and climatic niche differentiation. *Botanical Journal of the Linnean Society*, 182, 303–317. <https://doi.org/10.1111/boj.12419>
- Santos, J. C., Coloma, L. A., Summers, K., Caldwell, J. P., Ree, R., & Canatella, D. C. (2009). Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biology*, 7, e1000056.
- Sarmiento, G. (1992). Palinología de la Formación Guaduas-estratigrafía y sistemática. *Boletín Geológico Ingeominas*, 32, 45–126.
- Simon, M. F., Grether, R., de Quieroz, 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. *Proceedings of the National Academy of Sciences, USA*, 106, 20359–20364. <https://doi.org/10.1073/pnas.0903410106>
- Souza-Neto, A. C., Cianciaruso, M. V., & Collevatti, R. G. (2016). Habitat shifts shaping the diversity of a biodiversity hotspot through time: Insights from the phylogenetic structure of Caesalpinioideae in the Brazilian Cerrado. *Journal of Biogeography*, 43, 340–350. <https://doi.org/10.1111/jbi.12634>
- ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomao, R. P., & Guevara, J. E., ... Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, 342, e1243092. <https://doi.org/10.1126/science.1243092>
- Torres, V., Vandenberghe, J., & Hooghiemstra, H. (2005). An environmental reconstruction of the sediment infill of the Bogotá basin (Colombia) during the last 3 million years from abiotic and biotic proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 226, 127–148. <https://doi.org/10.1016/j.palaeo.2005.05.005>
- Van der Hammen, T., & García, C. (1966). The Paleocene pollen flora of Colombia. *Leidse Geologische Mededelingen*, 35, 105–114.
- Van der Hammen, T., Werner, J., & Dommelen, H. (1973). Palynologic record of the upheaval of the Northern Andes: A study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the Early evolution of its high-Andean biota. *Review of Palaeobotany and Palynology*, 16, 1–122. [https://doi.org/10.1016/0034-6667\(73\)90031-6](https://doi.org/10.1016/0034-6667(73)90031-6)
- Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, 6, e6848. <https://doi.org/10.1038/ncomms7848>
- Villagomez, D., & Spikings, R. (2013). Thermochronology and tectonics of the Central and Western Cordilleras of Colombia: Early Cretaceous-



- Tertiary evolution of the Northern Andes. *Lithos*, 160–161, 228–249. <https://doi.org/10.1016/j.lithos.2012.12.008>
- von Humboldt, A., & Bonpland, A. (1807). *Essay on the geography of plants- with a physical tableau of the equinoctial regions*. Chicago: University of Chicago Press.
- Webb, C. O., Ackerley, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics*, 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Wesselingh, F. P., Guerrero, J., Rasanen, M., Romero Pitmann, L., & Vonhif, H. (2006). Landscape evolution and depositional processes in the Miocene Amazonian Pebas lake/wetland system: Evidence from exploratory boreholes in northeastern Peru. *Scripta Geologica*, 133, 323–361.

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Author contributions: CDB designed the experiments and wrote the manuscript; CDB, CH and AA collected field and laboratory data; and CDB, FJVP and CH analysed the data. All authors contributed to and approved the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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