



Could coastal plants in western Amazonia be relicts of past marine incursions?

Abstract

The rainforests of Amazonia comprise some of the most biologically diverse ecosystems on Earth. Despite this high biodiversity, little is known about how landscape changes that took place in deep history have affected the assembly of its species, and whether the impact of such changes on biodiversity can still be observed. Here, we present a hypothesis to explain our observation that plants typical of Neotropical coastal habitats also occur in western Amazonia, in some cases thousands of kilometres away from the coast. Evidence on their current distribution, dispersal biology and divergence times estimated from molecular phylogenies suggest that these plants may be the legacy of the large marine-influenced embayment that dominated the area for millions of years in the Neogene. We hypothesize that coastal plants dispersed along the shores of this embayment and persisted as inland relicts after the marine incursion(s) retreated, probably with the aid of changes in soil conditions caused by the deposition of marine sediments. This dispersal corridor may also have facilitated the colonization of coastal environments by Amazonian lineages. These scenarios could imply an unexpected coastal source that has contributed to Amazonia's high floristic diversity and led to disjunct distributions across the Neotropics. We highlight the need for future studies and additional evidence to validate and shed further light on this potentially important pattern.

1 | INTRODUCTION

An embayment of more than one million km² covered western Amazonia in the Miocene, at least during intermittent periods between c. 23–10 Ma (Hoorn, 1993; Hoorn, Wesselingh, Hovikoski, & Guerrero, 2010; Hoorn, Wesselingh, ter Steege, et al., 2010; Hovikoski, Wesselingh, Räsänen, Gingras, & Vonhof, 2010; Hovikoski et al., 2007; Linhares, de Souza Gaia, & Feijó Ramos, 2017; Vonhof et al., 2003; Wesselingh, Guerrero, Räsänen, Romero Pittman, & Vonhof, 2006; Wesselingh et al., 2002). This embayment experienced marine influence, which likely originated from a Caribbean source (Boonstra, Ramos, Lammertsma, Antoine, & Hoorn, 2015; Jaramillo et al., 2017; Salamanca et al., 2016). In part, the marine influences are recognized in high frequency rhythmic sedimentary pulses that are characteristic of tidal conditions (Hovikoski et al., 2007, 2010). The relicts of this immense wetland system now constitute a fundamental part of the geological record of northern South America. Today, this region hosts some of the most species-rich

ecosystems on Earth. If aquatic—and especially marine—settings indeed dominated the region in the Miocene, this would have left a relatively short amount of time for the development of the region's high biodiversity (Antonelli et al., 2018; Tuomisto, Zuquim, & Cárdenas, 2014).

The evidence for marine influence in Amazonia derives from the fossil record of molluscs (Wesselingh et al., 2006), foraminifera, dinoflagellates, ostracods (Boonstra et al., 2015; Gross, Ramos, & Pillar, 2015; Jaramillo et al., 2017; Wesselingh & Ramos, 2010), mangrove pollen (Hoorn, 1993, 2006; Salamanca et al., 2016) as well as geochemical, ichnological and sedimentological data (Hovikoski et al., 2007; Jaramillo et al., 2017; Räsänen, Linna, Santos, & Negri, 1995; Vonhof et al., 2003). Amazonian lineages characteristic of marine environments include dolphins, manatees, sharks and stingrays (Bloom & Lovejoy, 2017; Jaramillo et al., 2017; Lovejoy, Albert, & Crampton, 2006). The existence of marine environments in Amazonia, and their influence on regional diversity, has been inferred from biogeographic analyses of amphibians (e.g. Santos et al., 2009), fish (e.g. Cooke, Chao, & Beheregaray, 2011) and plants (e.g. Antonelli, Nylander, Persson, & Sanmartin, 2009; Bacon, Velásquez-Puentes, Hoorn, & Antonelli, 2018; Freitas et al., 2016; Roncal, Kahn, Millan, Couvreur, & Pintaud, 2013; Snak et al., 2016).

Coastal plants are adapted to varying levels of salinity, strong currents and storm surges, exposure to sunlight and wind, high soil drainage capacity (sand) and/or low oxygen levels in the muddy and sandy soils that often associate with these environments (Lacerda et al., 1993; Wassilieff, 2012). Even if species grow further inland, they can be exposed to fluctuating conditions driven by intermittent exposure and rare events such as high cyclic tides and tropical storms. Typical elements in Neotropical estuarine systems include plant genera such as *Acrostichum*, *Dalbergia* and *Montrichardia* (Huber & Alarcón, 1988). Plants that are not salt tolerant but are commonly associated with estuaries include *Manicaria saccifera*, *Pachira aquatica*, *Phenakospermum guyannense*, *Pterocarpus officinalis*, *Symphonia globulifera* and *Virola surinamensis* (Behling, Cohen, & Lara, 2001; Dransfield et al., 2008; Huber & Alarcón, 1988; Urrego, Bernal, & Polania, 2009).

Here, we propose the hypothesis that the legacy of Miocene marine incursions in the region explains the present-day occurrence, in western Amazonia, of plant species found in coastal and/or estuarine zones. We explore several independent lines of evidence that appears to support our hypothesis, as discussed below. First, the distributions of these species within Amazonia largely fall within the

TABLE 1 Plant species occurring in modern estuarine environments, with disjunct populations in western Amazonia

Species	Family	Growth form	Dispersal vector	Distribution	Occurrence in South America								
					Pebas formation	W and N Guiana Shield	Napo river area	Lower Rio Negro area	Middle and upper Essequibo	Madre de Dios-Acre basins	Amazon River	Amazon delta	
<i>Acrostichum danaeifolium</i>	Pteridaceae	Herb	Wind, water? ¹	Pantropical	X				X				X
<i>Allamanda cathartica</i>	Apocynaceae	Climber, shrub	Water, wind ²	Neotropical	X	X	X						X
<i>Anemopaegma chrysoleucum</i>	Bignoniaceae	Liana	Water, wind ³	Neotropical	X	X	X		X				
<i>Bacris major</i>	Arecaceae	Clustered palm	Water? ⁴	Neotropical	X	X	X		X			X	X
<i>Carapa guianensis</i>	Meliaceae	Tree	Water, mammals ^{5,6}	Neotropical	X	X	X		X			X	X
<i>Cespedesia spathulata</i>	Ochnaceae	Tree	Wind, water? ⁷	Neotropical	X	X	X		X			X	
<i>Chrysobalanus icaco</i>	Chrysobalanaceae	Shrub	Water ⁸	Pantropical	X				X				X
<i>Dalbergia brownii</i>	Fabaceae/Faboideae	Shrub, liana, treelet	Water ⁷	SUSA + N South America	X	X	X		X				X
<i>Dalbergia ecataphyllum</i>	Fabaceae/Faboideae	Shrub	Water ⁹	Pantropical	X	X	X		X		X	X	X
<i>Dalbergia monetaria</i>	Fabaceae/Faboideae	Shrub, liana, treelet	Water ¹⁰	Neotropical	X	X	X		X		X	X	X
<i>Eperua falcata</i>	Fabaceae/Caesalpinioideae	Tree	Ballistic ¹¹	N South America	X	X	X		X				
<i>Guilandina bonduc</i>	Fabaceae/Caesalpinioideae	Climber	Water	Tropical + subtropical coasts	X				X				
<i>Hieronyma alchorneoides</i>	Euphorbiaceae	Tree	Fish, birds, mammals ^{12,13,14}	Neotropical	X	X	X		X				
<i>Machaenium lunatum</i>	Fabaceae/Faboideae	Shrub, climber	Water? ⁷	Neotropics + W Africa	X				X				
<i>Manicaria saccifera</i>	Arecaceae	Palm tree	Water ¹⁵	Neotropical	X	X	X		X				X
<i>Montichordia arborescens</i>	Araceae	Herb	Water ¹⁶	Neotropical	X	X	X		X			X	X
<i>Neptunia oleracea</i>	Fabaceae/Mimosoideae	Floating herb	Water ¹⁷	Pantropical	X				X			X	X
<i>Pachira aquatica</i>	Malvaceae	Tree	Water ¹⁸	Neotropical	X	X	X		X				X
<i>Pentaclethra macroloba</i>	Fabaceae/Mimosoideae	Tree	Ballistic + Water ¹⁹	Neotropical	X	X	X		X			X	X
<i>Phenakospermum guaymense</i>	Strelitziaceae	Arborescent herb	Water? birds?	N South America	X	X	X		X				
<i>Pterocarpus officinalis</i>	Fabaceae/Faboideae	Tree	Water ²⁰	Pantropical	X				X				
<i>Scragfolia amazonica</i>	Humiriaceae	Tree	Water ²¹	S-C America	X	X	X		X			X	X
<i>Sphagnetocola trilobata</i>	Asteraceae	Herb	Water ²²	Neotropical ⁸	X	X	X		X				
<i>Struchium sparganophorum</i>	Asteraceae	Herb	Water? ²³	Pantropical	X	X	X		X			X	
<i>Symphonia globulifera</i>	Cusciaceae	Tree	Birds, water mammals ^{24,25}	Neotropical, W Africa	X	X	X		X		X	X	X
<i>Terminalia amazonia</i>	Combretaceae	Tree	Water, wind ^{26,27}	Neotropical	X	X	X		X			X	
<i>Thalia geniculata</i>	Marantaceae	Herb	Water ²⁸	Neotropical	X				X			X	X
<i>Virola surinamensis</i>	Myristicaceae	Tree	Birds, fish, water ^{29,30}	Neotropical	X	X	X		X		X	X	X

Note. Where ¹indicates species that are invasive elsewhere.

- ¹Mahabale (1968). ²Alvarado-Cardenas and Ochoterena (2007). ³Smithsonian Tropical Research Institute. (2012). ⁴Galeano and Bernal (2010). ⁵McHargue and Hartshorn (1983). ⁶Scarano, Pereira, and Rôças (2003). ⁷Croat (1978). ⁸Penner (2004). ⁹Scarano (1998). ¹⁰Carvalho et al. (2011). ¹¹Forget (1989). ¹²Castro Lima (2009). ¹³Stevenson, Castellanos, Pizarro, and Garavito (2002). ¹⁴Orozco Zamora and Montagnini (2007). ¹⁵Burret (1928). ¹⁶Gordon and van der Valk (2003). ¹⁷Technigro. (2011). ¹⁸Alverson (1994). ¹⁹Williamson and Costa (2000). ²⁰Muller et al. (2009). ²¹Cuatrecasas (1961). ²²Thaman (2012). ²³Foster, Arce, and Wachter (1986). ²⁴Forget et al. (2007). ²⁵Dick and Heuertz (2008). ²⁶van Roosmalen (1985). ²⁷Muller-Landau, Wright, Calderón, Hubbell, and Foster (2002). ²⁸Mossman (2009). ²⁹Howe and Schupp (1985). ³⁰Moegenburg (2002).

geographic extent of the Miocene wetland. Second, time-calibrated molecular phylogenies of key species show that divergence between inland and coastal populations started only after the drainage of the wetland because dispersal is no longer possible between them. Third, the plant taxa investigated are distantly related and have different biogeographic histories, growth forms and dispersal abilities, thus raising the likelihood of shared historical factors underlying their current similar distributions.

Extant plants with a disjunct coastal and inland distribution and different ecologies (coastal, estuarine or both) may provide a previously unexplored data source to address the influence of historical landscape changes on the assembly of current ecosystems. Here, we assess multiple sources of data related to marine incursions that enable the development of a holistic understanding of the evolutionary history, and resulting distribution, of species in western Amazonia.

2 | CANDIDATE SPECIES

We chose an initial set of species by exploring lists of sea-drifted seeds and fruits that are Neotropical species from deltaic and/or estuarine environments (Armstrong, 2009; Burnham, 1990). We then excluded those species that have continental-wide distributions, resulting in 28 species which we refer to as 'candidate species' (Table 1). Candidate species are suggestive of deltaic and/or estuarine environments in the Neotropics, and that also occur disjunctly in western Amazonia. In coastal environments, these species are not strictly haline, but most of them grow at the upper end of the tidal belt (Seeliger, 1992). Candidate species belong to several distantly related lineages and have a variety of growth forms, including herbs, shrubs, trees and vines (Figure 1, Table 1). These are primarily water dispersed and one is also dispersed by fish, although a few others use additional dispersal agents not associated with water, such as birds, mammals or wind. Diaspores of several of the candidate species are commonly found among sea drift (Armstrong, 2009; Burnham, 1990). These characteristics make the candidate species particularly suitable as subjects to explore a possible link between current species distributions and past sea incursions.

3 | SPECIES DISTRIBUTIONS

Distribution records for the candidate species were sourced from public databases and herbaria (GBIF, INCT, COAH, INPA; downloaded on 17 December 2014) as well as from the literature (Database S1). Duplicate or erroneous records were removed as well as records with doubtful identifications or representing cultivated plants (*Allamanda cathartica* and *Chrysobalanus icaco*). The final number of South American occurrence records for subsequent analyses was 4,816, including 2,534 records of inland localities (External Database).

Species distribution maps were created in QGIS 2.6 (www.qgis.org) for Figure S1 and Diva-GIS 7.5 (www.diva-gis.org) for Figure 2. In Figure 2, candidate species richness was measured in one-degree grid cells. In Figure S1, we plotted the occurrence records for each species onto an environmental raster layer for the average value from all soil categories of total exchangeable bases (TEB) in cmol kg^{-1} (shown in green shading). Total exchangeable bases stand for the sum of exchangeable cations in soil (sodium [Na], calcium [Ca], magnesium [Mg] and potassium [K] in cmol kg^{-1}). Raster layers for soil environmental variables were created using the Harmonized World Soil Database (HWSD; <http://web.archive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/>; downloaded on February 18, 2015), using SQL, R and ArcGIS. The method is fully described at <https://wiki.biovel.eu/display/doc/BioVeL+Wiki>.

The highest concentration of candidate species (Figure 2) is found in the central part of western Amazonia, between Iquitos in Peru and Leticia in Colombia, where 23 species occur (Table 1). Farther north, near the Guiana Shield, an assemblage of 20 candidate species reaches the base of the Guianan escarpments, whereas 16 species occur along the middle and upper Essequibo River basin. There is a concentration of 13 candidate species in the border zone of Peru, Bolivia and Brazil, with up to nine species per square degree. Species in this zone include the water-dispersed *Pachira aquatica* and *Dalbergia monetaria*, and the pantropical seawater-dispersed *Dalbergia ecastaphyllum*, *Guilandina bonduc* and *Pterocarpus officinalis*. A high concentration of candidate species also occurs in the upper Napo River in eastern Ecuador, where 16 species occur, with up to 10 species per square degree.

The current distribution of the candidate species complements palaeogeographic reconstructions of the marine incursions in the periphery of the Guiana Shield (Hoorn, 2006; Hoorn, Wesselingh, ter Steege, et al., 2010; Hovikoski et al., 2007, 2010). This is indicated by the occurrence of 20 candidate species, some of which reach as far north as the upper Caura River in the Venezuelan Guiana (Figure 2; Table 1). Those that are exclusively water dispersed (e.g. *Pachira aquatica* and *Dalbergia ecastaphyllum*) provide the strongest indication for this interpretation.

An additional avenue for marine incursion along the Essequibo River (Hovikoski et al., 2010) (Figure 2) is also supported by the distribution of extant plants, as the candidate species reach far beyond the highest level of today's tides, c. 100 km upstream from its mouth (Worts, 1958). Although some of the species (*Hieronyma alchorneoides*, *Symphonia globulifera*, *Virola surinamensis*) have complementary dispersal agents such as mammals or birds, or an explosive discharge of the seeds from the fruit (*Pentaclethra maculoba*), occurrence of the seawater-dispersed *Dalbergia monetaria* and *Pterocarpus officinalis* (the latter of African origin and with pantropical estuarine distribution [Muller, Voccia, Ba, & Bouvet, 2009]) may indicate a marine incursion. However, the debated Essequibo-Rio Branco marine corridor (Hovikoski et al., 2010; Wesselingh & Hoorn, 2011) is not supported by the distribution of the candidate species, as represented by available herbarium collections.

The occurrence of 13 candidate species in the Madre de Dios and Acre basins, five of which are exclusively water dispersed, also suggests past marine influence in the region (e.g. the pantropical seawater-dispersed *Dalbergia ecastaphyllum*, *Guilandina bonduc* and *Pterocarpus officinalis*). During the late Miocene (c. 11.3–7 Ma), this area consisted of fluvial, deltaic and estuarine channel complexes (Hovikoski, 2006; Hovikoski et al., 2007; Räsänen et al., 1995), similar to the environments on the north-eastern coast of South America where these species are common today. A marine connection along the present-day Amazon River (e.g. Webb, 1995) is not supported by our data, as there is conspicuously low diversity of candidate plants along the Amazon east of its confluence with the Rio Negro (Figure 2; Table 1).

Can the observed distribution pattern of plants in Amazonia be an artefact caused by a geographic bias of collecting efforts? There are indeed large areas of Amazonia that have been poorly explored (Schulman, Toivonen, & Ruokolainen, 2007). However, the c. 5 million georeferenced plant occurrence records that we were able to access for this study through the Global Biodiversity Information Facility for the region (GBIF; Figure S2) show large, comparatively well-explored areas outside the proposed marine incursion area with low richness of candidate species, mostly 0–2 species per square degree of latitude–longitude. These areas include the middle Madeira, the lower Amazon, the Rio Branco and the Rio Negro. The few candidate species occurring in these areas are the trees *Carapa guianensis*, *Symphonia globulifera* or *Virola surinamensis*, which are both water- and mammal-dispersed.

Overall, the areas with the highest candidate species richness largely fit within the reconstruction of the Miocene incursion inferred from independent geological evidence (Figures 2, S1), although unequal sampling effort may occur amongst sites. In addition, these past marine incursion areas correspond approximately to where the highest soil cation concentrations are found today (Figure S1). Exceptions are seen where the marine sediments are covered by more recent, less cation-rich material, or where the recent sediments are equally or more cation-rich than those derived from the Pebas system due to, for example, the deposition of volcanic material by rivers (Higgins et al., 2011). A past marine connection between western Amazonia, the Guianas and the Orinoco delta can explain the affinities of extant candidate species among these areas. Recent independent arrivals of unrelated, mostly water-dispersed species across vast areas of dry land are unlikely, particularly for obligate water-dispersed species such as *Dalbergia ecastaphyllum*, *Dalbergia monetaria*, *Guilandina bonduc*, *Pachira aquatica* and *Pterocarpus officinalis*.

4 | MOLECULAR PHYLOGENETICS

DNA sequences were downloaded from the National Center for Biotechnology Information (GenBank) and complemented with new sequences (Table S2) for individuals from inland Amazonian and coastal populations of *Manicaria saccifera*. Those specimens were sequenced for the PRK and RPB2 genes following Bacon et al. (2016), and for the ITS and trnLF genes for *Pachira aquatica* following

the protocol of Duarte, Esteves, Salatino, Walsh, and Baum (2011). Divergence times were inferred for these two groups in BEAST 1.7.5 (Drummond, Ho, Phillips, & Rambaut, 2006) using a Yule tree prior and the GTR+ Γ model of nucleotide substitution with four gamma categories. Markov chains were sampled every 10,000th iteration for 100 million generations and repeated three times to test for Markov chain Monte Carlo convergence and to ensure effective sample sizes exceeded 200.

Internal nodes were calibrated to represent absolute time using fossil information. For the *Pachira* dataset, we estimated divergence times by constraining the phylogeny at the crown node of the Malvateca clade (Bombacoideae; Malvaceae) using *Malvaciphyllum macondicus* fossil leaves from the Cerrejón Palaeocene forests of Colombia (Carvalho, Herrera, Jaramillo, Wing, & Callejas, 2011). Synapomorphies were used to support natural affinities for the fossil leaves, allowing for robust placement in the phylogeny. We used an exponential prior defined by a mean of 0.7 and an offset value of 58 to account for uncertainty in the geological age of the fossil deposit following Carvalho et al. (2011) and to infer divergence times in *Pachira*. Exponential priors were also used to calibrate the palm topology where prior distributions were 1.0 and the offset value was set for the mean age of the respective palm fossils: *Attalea olsoni* (35 Ma), *Bactris pseudocuesco* (30 Ma), *Bactrites pandanifolius* (40 Ma), *Cocos* sp. (54.8 Ma), *Sabalites carolinensis* (85.8 Ma) and *Socratea brownii* (25 Ma), following Eiserhardt et al. (2011).

The mean crown ages for the two candidate species ranged from c. 9–2.5 Ma, indicating that these species had split from their sister groups and began to diverge only after the Miocene embayment had retreated. Once the conditions began to change, gene flow likely reduced and population differentiation and speciation may have begun. Our results suggest that gene flow occurred until the early Pliocene (5.0–4.3 Ma; Figure 3), when populations of both candidate species differentiated into Amazonian and coastal populations, due to increased isolation caused by the complete retreat of the embayment (only after c. 7 Ma).

Our results also suggest that dispersal may have been bidirectional, i.e., some species may have evolved in Amazonia or the foothills of the Guiana Shield and dispersed towards the coasts (*Pachira*; Carvalho-Sobrinho et al., 2016), while others dispersed from the present coastline towards the centre of the continent. For instance, the genus *Manicaria* originated in the middle Eocene c. 50 Ma (Figure 3), and several lines of evidence suggest that it evolved in the Guiana Shield and coastal Atlantic region. First, the two species currently recognized in the genus are distributed in this area. Second, the Guiana Shield comprises the distributional area of tribe Leopoldinieae, the sister group of tribe Manicarieae to which *Manicaria* belongs (Baker et al., 2009; Dransfield et al., 2008), and may also have harboured the ancestors of extant *Geonoma*, the sister group of Manicarieae plus Leopoldinieae (Roncal, Borchsenius, Asmussen-Lange, & Balslev, 2010). Third, the only known highland populations of *Manicaria* are found in the Guiana Shield, reaching up to 1,225 m. Fourth, dichotomously branched stems in palms (like



FIGURE 1 The candidate species suggestive of deltaic/or estuarine environments in western Amazonia surveyed in this study represent different lineages and growth forms. (a) The fern *Acrostichum danaeifolium* (Pteridaceae); (b), the tree *Cespedesia spatulata* (Ochnaceae); (c) the shrub *Chrysobalanus icaco* (Chrysobalanaceae); (d) the climber *Guilandina bonduc* (Fabaceae); (e) the palm *Manicaria saccifera* (Arecaceae); (f) the creeping herb *Sphagneticola trilobata* (Asteraceae). All photographs by R. Bernal

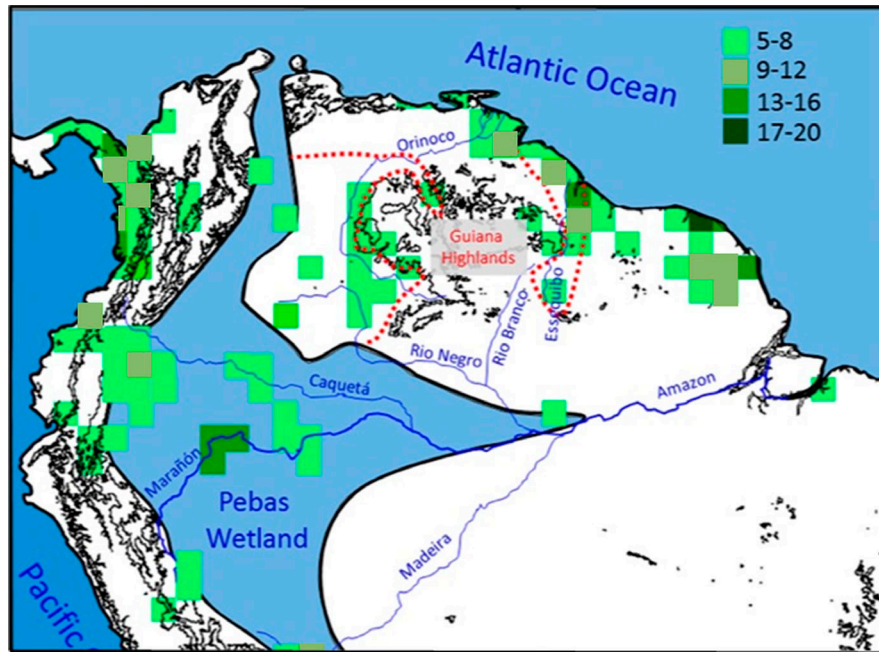


FIGURE 2 Extant records of candidate plants with deltaic/marine/estuary characteristics in South America mapped using Diva-GIS 7.5 (www.diva-gis.org). Colors represent the number of candidate species in one-degree cells. The possible extent of wetlands is based on a compilation of published reconstructions and a mid-Miocene palaeogeographic map. Relief and continent contour correspond to present conditions; in blue the reconstructed Pebas wetland. The red dotted line represents areas where estuarine, exclusively water-dispersed plants also occur, and have been postulated as additional areas of marine embayments^{2,10}. Only grids with >4 candidate species are shown, in order to reduce noise caused by species with additional dispersal strategies besides water

those of trans-Andean populations of *Manicaria*) are considered derived from unbranched stems like those in Amazonian and other cis-Andean populations (Fisher & Maidman, 1999). Our results from the dated *Manicaria* phylogeny suggest that the species originated along the Atlantic coast, dispersed into Amazonia and likely became isolated from the coastal populations after the embayment retreated and transformed into the Amazon fluvial system ('Acre System' in the sedimentary record; Figure 3; Hoorn, Wesselingh, Hovikoski, et al., 2010).

5 | PLANTS AS RELICTS OF MARINE INCURSIONS?

The different lines of evidence explored here indicate the potential for a common historical and evolutionary scenario. Our hypothesis is that these candidate plant species growing in western Amazonia are, in a sense, living fossils that can help us to understand the interactions between landscape changes and biodiversity. The current distribution of candidate species and their patterns of richness underscore the interplay between biota and landscape processes, including Andean mountain building and marine incursions (Eakin, Lithgow-Bertelloni, & Dávila, 2014; Hoorn, Wesselingh, ter Steege, et al., 2010; Hoorn et al., 2017; Shepard, Müller, Liu, & Gurnis, 2010; van Soelen et al., 2017).

The species discussed here are evidence of extant terrestrial organisms associated to past marine incursions. However, they

may well be just the tip of an iceberg—a mere indication of the pivotal role of past coastal settings in shaping Amazonia's present biota. Further research should aim at investigating the general importance of these findings on the whole Amazonian flora, through the integration of molecular, palaeontological and environmental data. Specifically, we suggest a careful review of the fossil pollen of the candidate species. A major contribution would be to relate these with their nearest living relative and trace the effect of marine incursions on plant diversity and distribution. Second, key insight would be gained by untangling the effect of marine from orogenic, edaphic or climatic-induced variables on the distribution and diversification of species. To achieve this, it will be pivotal to design numerical climate simulations accounting for the actual Miocene palaeogeography (i.e. palaeotopography and wetlands extent). By translating the reconstruction of the Pebas wetland (Boonstra et al., 2015; Hernández et al., 2005; Hoorn, Wesselingh, ter Steege, et al., 2010; Jaramillo et al., 2017) on a published mid-Miocene topographic map (Herold, Seton, Muller, You, & Huber, 2008), we provide a realistic physiographic Miocene context for South America that will be useful for such a purpose (Figure S3). Ultimately, these contributions will allow us to better ascertain to what extent the current abiotic environment (e.g. Ritter et al., 2018) has influenced the relictual signals from past marine incursions. Lastly, dense phylogeographic sampling would lead to explicit tests of the geographic origin, genetic diversity and population structure of the candidate plant species.

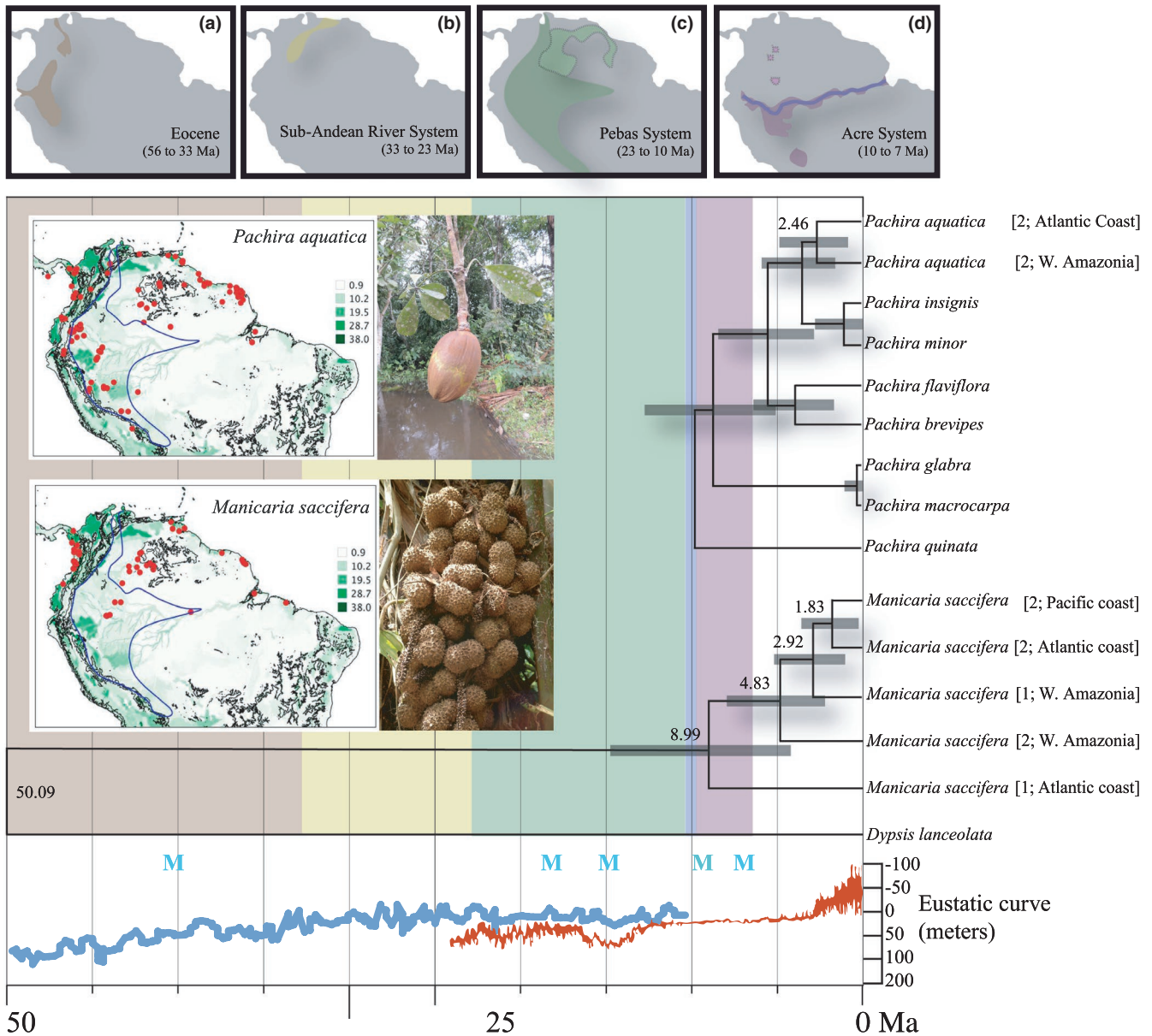


FIGURE 3 Phylogenetic relationships of coastal and inland populations of the tree *Pachira aquatica* and the palm *Manicaria saccifera* based on DNA sequences. The number in brackets represents the number of individuals sampled per geographic area, also listed (Atlantic, Pacific coast, and Amazonia). The two species are depicted to the left of the phylogeny (photographs by R. Bernal), together with their geographic distribution (red dots) mapped onto soil fertility (total exchangeable bases, cmol/kg, green shading) using QGIS 2.6 (www.qgis.org) and the reconstructed Pebas wetland, according to this study, is shown in blue contour (see also Fig. S1). The timing of divergence is listed at nodes and bars show credibility intervals in age estimates. Four periods of aquatic systems in South America are mapped: (a) follows Louterbach et al. (2014) and (b–d) follow results presented here and in Hoorn, Wesselingh, ter Steege, et al. (2010). The putative extension of the Pebas wetland into the Orinoco region (as suggested by the occurrence of estuarine, water-dispersed plants) is in light green and the onset of the Amazon River at c. 9 Ma is shown with a blue line (Hoorn et al., 2017). Below the phylogeny, six known periods of marine events are depicted with an 'M' (Jaramillo et al., 2017; Salamanca et al., 2016). Global sea level, following Miller, Mountain, Wright, and Browning (2011) in blue and Higgins et al. (2011) in red, is shown at the bottom of the figure

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COMPETING INTERESTS

The authors declare that they have no competing interests.


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SUPPORTING INFORMATION

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

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