



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
<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
<i>Carapa guianensis</i>	Meliaceae	Tree	Water, mammals ^{5,6}	Neotropical	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						
<i>Dalbergia ecastaphyllum</i>	Fabaceae/Faboideae	Shrub	Water ⁹	Pantropical	X	X	X		X		X		X
<i>Dalbergia monetaria</i>	Fabaceae/Faboideae	Shrub, liana, treelet	Water ¹⁰	Neotropical	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								
<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		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		X		X
<i>Pterocarpus officinalis</i>	Fabaceae/Faboideae	Tree	Water ²⁰	Pantropical	X			X	X				
<i>Scopafolhis 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					
<i>Struchium sparganophorum</i>	Asteraceae	Herb	Water? ²³	Pantropical	X		X		X		X		
<i>Symphonia globulifera</i>	Cusciaceae	Tree	Birds, water mammals ^{24,25}	Neotropical, W Africa	X	X	X		X		X		X
<i>Terminalia amazonia</i>	Combretaceae	Tree	Water, wind ^{26,27}	Neotropical	X	X	X		X		X		X
<i>Thalia geniculata</i>	Marantaceae	Herb	Water ²⁸	Neotropical	X				X				X
<i>Virola surinamensis</i>	Myristicaceae	Tree	Birds, fish, water ^{29,30}	Neotropical	X	X	X		X		X		X

Note. Where ³¹indicates species that are invasive elsewhere.

- ¹Mahabale (1968). ²Alvarado-Cardenas and Ochotrena (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 Roomalen (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 Malvatheca 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 spathulata* (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 [Colour figure can be viewed at wileyonlinelibrary.com]

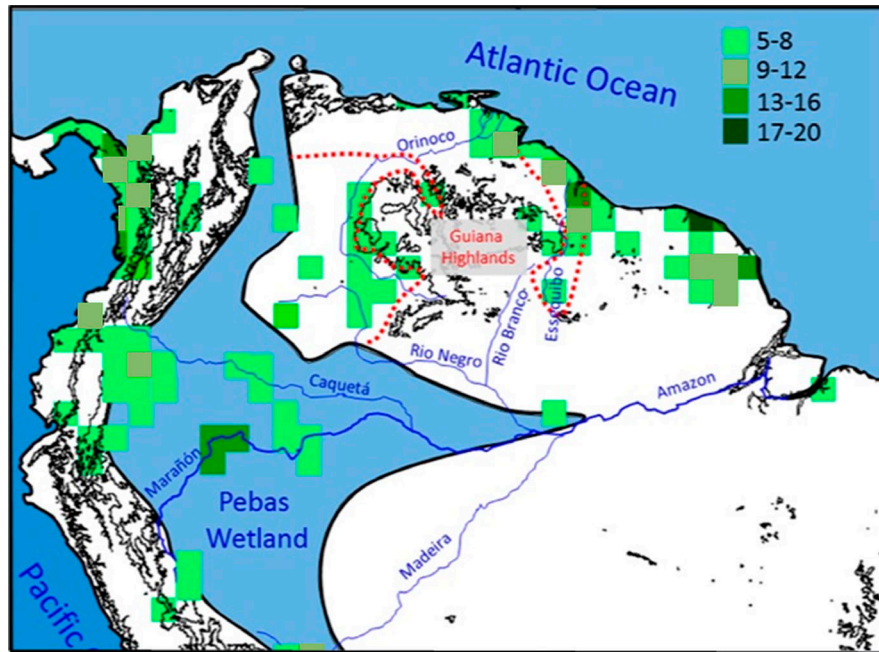


FIGURE 2 Extant records of candidate plants with deltaic/marine/estuary characteristics in South America mapped using Diva-GIS 7.5 (www.diva-gis.org). Colors represent the number of candidate species in one-degree cells. The possible extent of wetlands is based on a compilation of published reconstructions 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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.

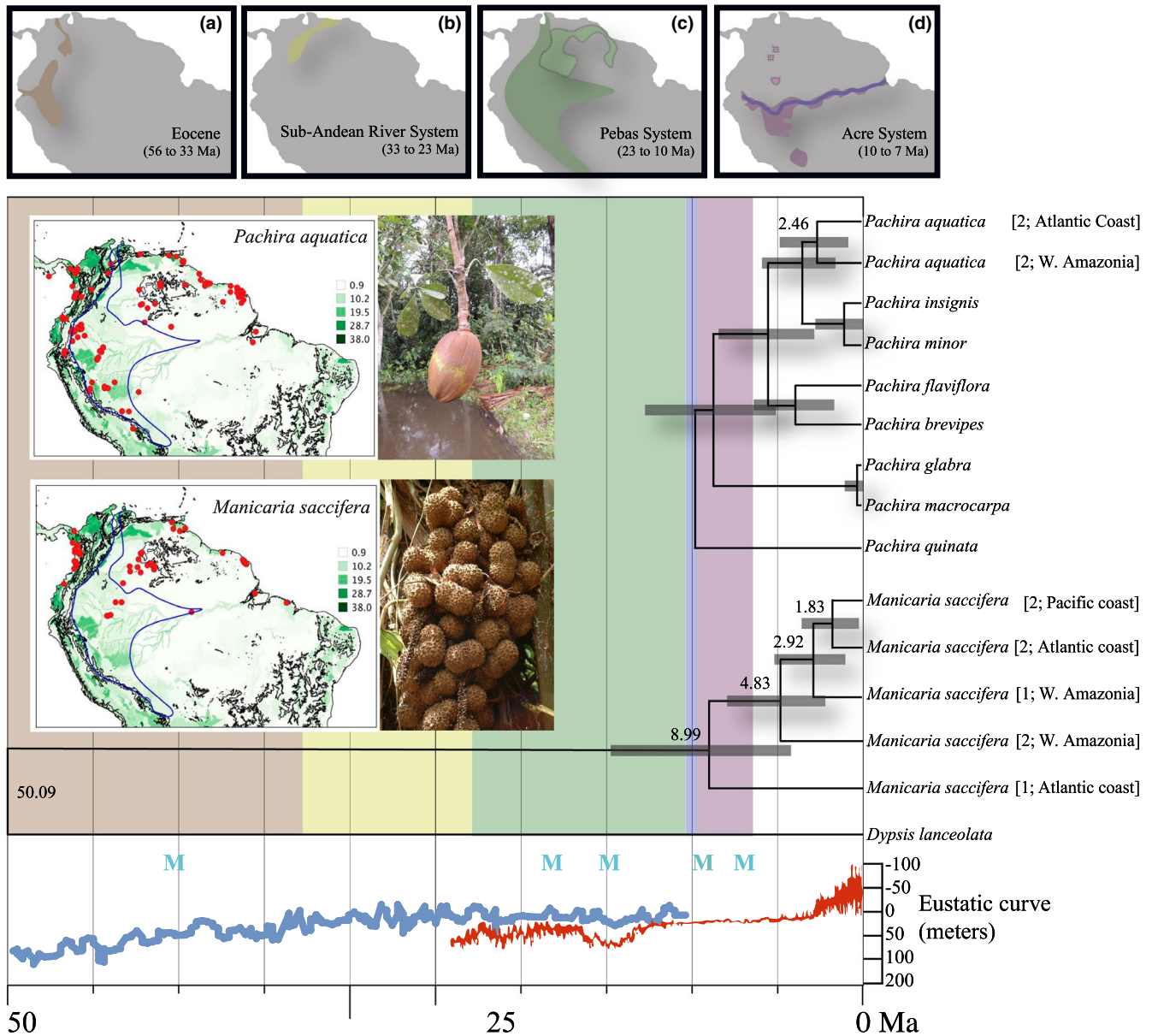


FIGURE 3 Phylogenetic relationships of coastal and inland populations of the tree *Pachira aquatica* and the palm *Manicaria saccifera* based on DNA sequences. The number in brackets represents the number of individuals sampled per geographic area, also listed (Atlantic, Pacific coast, and Amazonia). 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 [Colour figure can be viewed at wileyonlinelibrary.com]

ACKNOWLEDGEMENTS

This research originated during fieldwork of R.B. and H.B. for the project Palm Harvest Impacts in Tropical Forest—PALMS (FP7-ENB-2007-1; EU Grant Agreement 212631 and the Danish Council for Independent Research—Natural Sciences (4181-00158) to H.B.,

an Investissement d'Avenir grant of the French ANR (CEBA: ANR-10-LABX-0025) to C.D.B., and the Swedish Research Council (B0569601), the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013, ERC Grant Agreement 331024), the Swedish Foundation for Strategic Research and a Wallenberg Academy Fellowship to AA. We thank J. Chave,

C. Lafleur, P. Gaucher and D. Deslignes for support with fieldwork in French Guiana, the Alexander von Humboldt Institute, Jéssica Gómez and Ignacio Sánchez for support with fieldwork in Colombia and J. A. Diniz-Filho and Christopher Dick for valuable discussions. We thank F. Quevedo and R. Giovanni for support with the implementation of soil environmental layers.

Email: rgbernal@gmail.com

*These authors contributed equally to this work.

COMPETING INTERESTS

The authors declare that they have no competing interests.


ORCID

Christine D. Bacon  <https://orcid.org/0000-0003-2341-2705>

Hanna Tuomisto  <https://orcid.org/0000-0003-1640-490X>

Keywords

biodiversity, fossil, marine incursions, Neogene, phylogeny, South America

Rodrigo Bernal^{1*}
Christine D. Bacon^{2,3*} 

Henrik Balslev⁴

Carina Hoorn^{5,6}

Sarah J. Bourlat⁷

Hanna Tuomisto⁸ 

Sonia Salamanca⁹

Milan Teunissen van Manen⁵

Ingrid Romero^{10,11}

Pierre Sepulchre¹²

Alexandre Antonelli^{1,2,13}

¹Reserva Natural Guadualito, Montenegro, Quindío, Colombia

²Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

³Gothenburg Global Biodiversity Centre, Gothenburg, Sweden

⁴Department of Bioscience, Aarhus University, Aarhus C, Denmark

⁵Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park, The Netherlands

⁶KIAM, Universidad Regional Amazonica, Parroquia Muyuna, Tena, Napo, Ecuador

⁷Centre for Molecular Biodiversity Research, Zoological Research Museum Alexander Koenig (ZFMK), Bonn, Germany

⁸Department of Biology, University of Turku, Turku, Finland

⁹Ida Gerhardtlaan 9, Heemstede, The Netherlands

¹⁰Smithsonian Tropical Research Institute, Balboa, Panama

¹¹Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois

¹²Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA- CNRS-UVSQ, Université Paris-Saclay, Gif-sur-Yvette, France

¹³Gothenburg Botanical Garden, Gothenburg, Sweden

Correspondence

Rodrigo Bernal, Reserva Natural Guadualito, Montenegro, Quindío, Colombia.

REFERENCES

- Alvarado-Cardenas, L. O., & Ochoterena, H. (2007). A phylogenetic analysis of the Cascabela-Thevetia species complex (Plumeriaceae, Apocynaceae) based on morphology. *Annals of the Missouri Botanical Garden*, 94, 298–323. [https://doi.org/10.3417/0026-6493\(2007\)94\[298:APAOTC\]2.0.CO;2](https://doi.org/10.3417/0026-6493(2007)94[298:APAOTC]2.0.CO;2)
- Alverson, W. S. (1994). New species and combinations of *Catostemma* and *Pachira* (Bombacaceae) from the Venezuelan Guayana. *Novon*, 4, 3–8. <https://doi.org/10.2307/3391688>
- Antonelli, A., Nylander, J. A. A., Persson, C., & Sanmartin, 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., Zizka, A., Antunes Carvalho, F., Scharn, R., Bacon, C. D., Silvestro, D., & Condamine, F. (2018). Amazonia is the primary source of Neotropical biodiversity. *Proceedings of the National Academy of Sciences, USA*, 115, 6034–6039. <https://doi.org/10.1073/pnas.1713819115>
- Armstrong, W. P. (2009). *Drift seeds and drift fruits: Seeds that ride the ocean currents*. Retrieved from <http://waynesword.palomar.edu/pldec398.htm>
- Bacon, C. D., Velásquez-Puentes, F., Flórez-Rodríguez, A., Balslev, H., Galeano, G., Bernal, R., & Antonelli, A. (2016). Phylogeny of Iriarteeae palms, 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>
- Bacon, C. D., Velásquez-Puentes, F. J., Hoorn, C., & Antonelli, A. (2018). Iriarteeae palms tracked the uplift of Andean Cordilleras. *Journal of Biogeography*, 45, 1653–1663. <https://doi.org/10.1111/jbi.13350>
- Baker, W. J., Savolainen, V., Asmussen-Lange, C. B., Chase, M. W., Dransfield, J., Forest, F., ... Wilkinson, M. (2009). Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology*, 58, 240–256. <https://doi.org/10.1093/sysbio/syp021>
- Behling, H., Cohen, M. C. L., & Lara, R. J. (2001). Studies on Holocene mangrove ecosystem dynamics of the Bragança Peninsula in north-eastern Para, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 167, 225–242. [https://doi.org/10.1016/S0031-0182\(00\)00239-X](https://doi.org/10.1016/S0031-0182(00)00239-X)
- Bloom, D. D., & Lovejoy, N. R. (2017). On the origins of marine-derived freshwater fishes in South America. *Journal of Biogeography*, 44, 1927–1938. <https://doi.org/10.1111/jbi.12954>
- Boonstra, M., Ramos, M. I. F., Lammertsma, E. I., Antoine, P.-O., & Hoorn, C. (2015). Marine connections of Amazonia: Evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 417, 176–194. <https://doi.org/10.1016/j.palaeo.2014.10.032>
- Burnham, R. J. (1990). Paleobotanical implications of drifted seeds and fruits from modern mangrove litter, Twin Cays, Belize. *Palaios*, 5, 364–370. <https://doi.org/10.2307/3514892>
- Burret, M. (1928). Die Palmengattung *Manicaria* Gaertn. *Notizblatt des Botanischen Gartens und Museums Zu Berlin-Dahlem*, 10, 389–394. <https://doi.org/10.2307/3994653>
- Carvalho, M. R., Herrera, F. A., Jaramillo, C. A., Wing, S. L., & Callejas, R. (2011). Paleocene Malvaceae from northern South America and their biogeographical implications. *American Journal of Botany*, 98, 1337–1355. <https://doi.org/10.3732/ajb.1000539>
- Carvalho-Sobrinho, J. G., Alverson, W. S., Alcántara, S., Queiroz, L. P., Mota, A. C., & Baum, D. A. (2016). Revisiting the phylogeny of Bombacoideae (Malvaceae): Novel relationships, morphologically



- cohesive clades, and a new tribal classification based on multilocus phylogenetic analyses. *Molecular Phylogenetics and Evolution*, *101*, 56–74. <https://doi.org/10.1016/j.ympev.2016.05.006>
- Castro Lima, F. A. (2009). Frutos, semillas, y flores consumidos por peces de la Orinoquía, Colombia. Rapid Color Guide 248, The Field Museum, Chicago. Retrieved from http://fm2.fieldmuseum.org/plantguides/guide_pdfs/248%20Frutos%20de%20Peces%201.pdf
- Cooke, G. M., Chao, N. L., & Beheregaray, L. B. (2011). Marine incursions, cryptic species and ecological diversification in Amazonia: The biogeographic history of the croaker genus *Pasgioscion* (Sciaenidae). *Journal of Biogeography*, *39*, 724–738.
- Croat, T. B. (1978). *Flora of Barro Colorado Island*. Stanford, CA: Stanford University Press.
- Cuatrecasas, J. (1961). A taxonomic revision of the Humiriaceae. *Contributions from the United States National Herbarium*, *35*, 25–214.
- Dick, C. W., & Heuertz, M. (2008). The complex biogeographic history of a widespread tropical tree species. *Evolution*, *62*–11, 2760–2774. <https://doi.org/10.1111/j.1558-5646.2008.00506.x>
- Dransfield, J., Uhl, N., Asmussen, C., Baker, W., Harley, M., & Lewis, C. (2008). *Genera Palmarum: The evolution and classification of palms*. Richmond, UK: Kew Publishing.
- Drummond, A. J., Ho, S. Y. W., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology* *4*, e88. <https://doi.org/10.1371/journal.pbio.0040088>
- Duarte, M. C., Esteves, G. L., Salatino, M. L. F., Walsh, K. C., & Baum, D. A. (2011). Phylogenetic analysis of *Eriotheca* and related genera (Bombacoideae, Malvaceae). *Systematic Botany*, *36*, 690–701. <https://doi.org/10.1600/036364411X583655>
- Eakin, C. M., Lithgow-Bertelloni, C., & Dávila, F. M. (2014). Influence of Peruvian flat-subduction dynamics on the evolution of western Amazonia. *Earth and Planetary Science Letters*, *404*, 250–260. <https://doi.org/10.1016/j.epsl.2014.07.027>
- Eiserhardt, W. L., Pintaud, J.-C., Asmussen-Lange, C. B., Hahn, W. J., Bernal, R., & Balslev, H. (2011). Phylogeny and divergence times of Bactridinae (Arecaceae, Palmae) based on plastid and nuclear DNA sequences. *Taxon*, *60*, 485–498. <https://doi.org/10.1002/tax.602016>
- Fisher, J., & Maidman, K. J. (1999). Branching and architecture in palms. In A. Henderson & F. Borchsenius (Eds.), *Evolution, variation and classification of palms* (pp. 35–46). Bronx, NY: New York Botanical Garden Press.
- Forget, P.-M. (1989). Natural regeneration of an autochorous species of the Guianese forest, *Eperua falcata* Aublet (Caesalpinaceae). *Biotropica*, *21*(2), 115–125. <https://doi.org/10.2307/2388702>
- Forget, P.-M., Dennis, A. J., Mazer, S. J., Janzen, P. A., Kitamura, S., Lambert, J. E., & Westcott, D. A. (2007). Seed allometry and disperser assemblages in tropical reforests: A comparison of four floras in different continents. In A. J. Dennis, E. W. Schupp, R. A. Green, & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 5–36). Wallingford, UK: CABI. <https://doi.org/10.1079/9781845931650.0000>
- Foster, R. B., Arce, J. B., & Wachter, T. S. (1986). Dispersal and the sequential plant communities in Amazonian Peru floodplain. In A. Estrada & T. H. Fleming (Eds.), *Frugivores and seed dispersal* pp. (357–370). Dordrecht, The Netherlands: Springer. <https://doi.org/10.1007/978-94-009-4812-9>
- Freitas, C., Meerow, A. W., Pintaud, J.-C., Henderson, A., Noblick, L., Costa, F. R. C., ... Barrington, D. (2016). Phylogenetic analysis of *Attalea* (Arecaceae): Insights into the historical biogeography of a recently diversified Neotropical plant group. *Botanical Journal of the Linnean Society*, *182*, 287–302. <https://doi.org/10.1111/bj.12466>
- Galeano, G., & Bernal, R. (2010). *Palmas de Colombia. Guía de Campo*. Bogota, Colombia: Instituto de Ciencias Naturales, Universidad Nacional de Colombia.
- Gordon, E., & van der Valk, A. G. (2003). Secondary seed dispersal in *Montrichardia arborescens* (L.) Schott dominated wetlands in laguna grande, Venezuela. *Plant Ecology*, *168*, 177–190. <https://doi.org/10.1023/A:1024421324294>
- Gross, M., Ramos, M. I. F., & Piller, W. E. (2015). A minute ostracod (Crustacea: Cytheromatidae) from the Miocene Solimoes Formation (western Amazonia, Brazil): Evidence for marine incursions? *Journal of Systematic Paleontology*, *14*, 581–602.
- Hernández, R. M., Jordan, T. E., Dalenz Farjat, A., Echavarría, L., Idleman, B. D., & Reynolds, J. H. (2005). Age, distribution, tectonics, and eustatic controls of the Paranaense and Caribbean marine transgressions in southern Bolivia and Argentina. *Journal of South American Earth Sciences*, *19*, 495–512. <https://doi.org/10.1016/j.jsames.2005.06.007>
- Herold, N., Seton, M., Muller, R. D., You, Y., & Huber, M. (2008). Middle Miocene tectonic boundary conditions for use in climate models. *Geochemistry, Geophysics, Geosystems*, *9*. <https://doi.org/10.1029/2008GC002046>
- Higgins, M. A., Ruokolainen, K., Tuomisto, H., Llerena, N., Cardenas, G., Phillips, O. L., ... Räsänen, M. E. (2011). Geological control of floristic composition in Amazonian forests. *Journal of Biogeography*, *38*, 2136–2149. <https://doi.org/10.1111/j.1365-2699.2011.02585.x>
- 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. (2006). Mangrove forests and marine incursions in Neogene Amazonia (Lower Apaporis River, Colombia). *Palaeos*, *21*, 197–209. <https://doi.org/10.2110/palo.2005.p05-131>
- 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., Wesselingh, F., Hovikoski, J., & Guerrero, J. (2010). The development of the Amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In C. Hoorn & F. Wesselingh (Eds.), *Amazonia, landscape and species evolution: A look into the past* (pp. 123–142). Oxford, UK: Blackwell Publishing.
- Hoorn, C., Wesselingh, 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>
- Hovikoski, J. (2006). *Miocene Western Amazonia in the light of sedimentological and ichnological data*. Turku, Finland: University of Turku.
- Hovikoski, J., Gingras, M., Räsänen, M. E., Rebata, L. A., Guerrero, J., Ranzi, A., ... Lopez, S. (2007). The nature of Miocene Amazonian epicontinental embayment: High-frequency shifts of the low-gradient coastline. *Geological Society of America Bulletin*, *119*, 1506–1520. [https://doi.org/10.1130/0016-7606\(2007\)119\[1506:TNOMAE\]2.0.CO;2](https://doi.org/10.1130/0016-7606(2007)119[1506:TNOMAE]2.0.CO;2)
- Hovikoski, J., Wesselingh, F., Räsänen, M. E., Gingras, M., & Vonhof, H. B. (2010). Marine influence in Amazonia: Evidence from the geological record. In C. Hoorn & F. Wesselingh (Eds.), *Amazonia, landscape and species evolution: A look into the past* (pp. 143–161). Oxford, UK: Blackwell Publishing.
- Howe, H. F., & Schupp, E. W. (1985). Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology*, *66*, 781–791. <https://doi.org/10.2307/1940539>
- Huber, O., & Alarcón, C. (1988). Mapa de vegetación de Venezuela. *Escala 1:2.000.000*. Caracas, Venezuela: Ministerio de los Recursos Naturales Renovables/The Nature Conservancy.
- Jaramillo, C., Romero, I., D'Apolito, C., Bayona, G., Duarte, E., Louwye, S., ... Wesselingh, F. P. (2017). Miocene flooding events of western

- Amazonia. *Science Advances*, 3, e1601693. <https://doi.org/10.1126/sciadv.1601693>
- Lacerda, L. D., Conde, J. E., Alarcon, C., Alvarez-León, R., Bacon, P. R., D'Croz, L., ... Vannucci, M. (1993). Mangrove ecosystems of Latin America and the Caribbean: A summary. In pp. 1–42. International Society for Mangrove Ecosystems.
- Linhares, A. P., de Souza Gaia, V., & Feijó Ramos, M. I. (2017). The significance of marine microfossils for paleoenvironmental reconstruction of the Solimões Formation (Miocene), western Amazonia, Brazil. *Journal of South American Earth Sciences*, 79, 57–66. <https://doi.org/10.1016/j.jsames.2017.07.007>
- Louterbach, M., Roddaz, M., Bailleul, J., Antoine, P.-O., Adnet, S., Kim, J. H., ... Baby, P. (2014). Evidences for a Paleocene marine incursion in southern Amazonia (Madre de Dios Sub-Andean Zone, Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 414, 451–471. <https://doi.org/10.1016/j.palaeo.2014.09.027>
- Lovejoy, N. R., Albert, J. S., & Crampton, W. G. R. (2006). Miocene marine incursions and marine/freshwater transitions: Evidence from Neotropical fishes. *Journal of South American Earth Sciences*, 21, 5–13. <https://doi.org/10.1016/j.jsames.2005.07.009>
- Mahabale, T. S. (1968). Spores and pollen grains of water plants and their dispersal. *Review of Palaeobotany and Palynology*, 7, 285–296. [https://doi.org/10.1016/0034-6667\(68\)90034-1](https://doi.org/10.1016/0034-6667(68)90034-1)
- McHargue, L. A., & Hartshorn, G. S. (1983). Seed and seedling ecology of *Carapa guianensis*. *Turrialba*, 33, 399–404.
- Miller, K. G., Mountain, G. S., Wright, J. D., & Browning, J. V. (2011). A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography*, 24, 40–53. <https://doi.org/10.5670/oceanog>
- Moegenburg, S. M. (2002). Spatial and temporal variation in hydrochory in Amazonian floodplain forest. *Biotropica*, 34, 606–612. <https://doi.org/10.1111/j.1744-7429.2002.tb00581.x>
- Mossman, R. E. (2009). Seed dispersal and reproduction patterns among everglades plants. FIU Electronic Theses and Dissertations. Paper 135.
- Muller, F., Voccia, M., Ba, A., & Bouvet, J.-M. (2009). Genetic diversity and gene flow in a Caribbean tree *Pterocarpus officinalis* Jacq.: A study based on chloroplast and nuclear microsatellites. *Genetics*, 135, 185–198.
- Muller-Landau, H. C., Wright, S. J., Calderón, O., Hubbell, S. P., & Foster, R. B. (2002). Assessing recruitment limitation: Concepts, methods and case-studies from a tropical forest. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology* (pp. 35–53). London, UK: Evolution and Conservation. CAB International.
- Orozco Zamora, C., & Montagnini, F. (2007). Lluvia de semillas y sus agentes dispersores en plantaciones forestales de nueve especies nativas en parcelas puras y mixtas en la Estación Biológica La Selva, Costa Rica. *Recursos Naturales y Ambiente*, 49(50), 131–140.
- Räsänen, M. E., Linna, A. M., Santos, J. C. R., & Negri, F. R. (1995). Late Miocene tidal deposits in the Amazonian foreland basin. *Science*, 269, 386–390. <https://doi.org/10.1126/science.269.5222.386>
- Renner, S. (2004). Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences*, 165(4 Suppl.), S23–S33. <https://doi.org/10.1086/383334>
- Ritter, C. D., Zizka, A., Barnes, C., Nilsson, R. H., Roger, F., & Antonelli, A. (2018). Locality or habitat? Exploring predictors of biodiversity in Amazonia. *Ecography*, 41, e1–e13.
- Roncal, J., Borchsenius, F., Asmussen-Lange, C. B., & Balslev, H. (2010). Divergence times in the tribe Geonomateae (Arecaceae) coincide with Tertiary geological events. In O. Seberg, G. Pederson, A. S. Barfod & J. I. Davis (Eds.), *Diversity, phylogeny, and evolution of the monocotyledons* (pp. 245–265). Aarhus, Denmark: Aarhus University Press.
- 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>
- Salamanca, S., van Soelen, E. E., Teunissen van Manen, M. L., Flantua, S. G. A., Ventura Santos, R., Roddaz, M., ... Hoorn, C. (2016). Amazon forest dynamics under changing abiotic conditions in the early Miocene (Colombia Amazonia). *Journal of Biogeography*, 43, 2424–2437. <https://doi.org/10.1111/jbi.12769>
- Santos, J. C., Coloma, L. A., Summers, K., Caldwell, J. P., Ree, R., & Cannatella, D. C. (2009). Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biology*, 7, e1000056.
- Scarano, F. R. (1998). A comparison of dispersal, germination and establishment of woody plants subjected to distinct flooding regimes in Brazilian flood-prone forests and estuarine vegetation. In F. R. Scarano & A. C. Franco (Eds.), *Ecophysiological strategies of xerophytic and amphibious plants in the Neotropics*. Series Oecologia Brasiliensis 4 (pp. 177–193). Rio de Janeiro, Brazil: PPGE-UFRJ.
- Scarano, F. R., Pereira, T. S., & Rôças, G. (2003). Seed germination during floatation and seedling growth of *Carapa guianensis*, a tree from flood-prone forests of the Amazon. *Plant Ecology*, 168, 291–296. <https://doi.org/10.1023/A:1024486715690>
- Schulman, L., Toivonen, T., & Ruokolainen, K. (2007). Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography*, 34, 1388–1399. <https://doi.org/10.1111/j.1365-2699.2007.01716.x>
- Seeliger, U. (1992). *Coastal plant communities of Latin America*. San Diego, CA: Academic Press.
- Shepard, G. E., Müller, R. D., Liu, L., & Gurnis, M. (2010). Miocene drainage reversal of the Amazon River driven by plate-mantle interaction. *Nature Geoscience*, 3, 870–875. <https://doi.org/10.1038/ngeo1017>
- Smithsonian Tropical Research Institute. (2012). Environmental Science Program. Retrieved from <http://stri.si.edu/sites/esp/tesp/details.php?id=867>.
- Snak, C., Vatanparast, M., Silva, C., Lewis, G. P., Lavin, M., Kajita, T., & Paganucci de Quieroz, L. (2016). A dated phylogeny of the papilionoid legume genus *Canavalia* reveals recent diversification by a pantropical liana lineage. *Molecular Phylogenetics and Evolution*, 98, 133–146. <https://doi.org/10.1016/j.ympev.2016.02.001>
- Stevenson, P. R., Castellanos, M. C., Pizarro, J. C., & Garavito, M. (2002). Effects of seed dispersal by three Ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology*, 23, 1187–1204. <https://doi.org/10.1023/A:1021118618936>
- Technigro. (2011). Water mimosa (*Neptunia oleracea*). Retrieved from <http://www.technigro.com.au/documents/WW%20Water%20mimosa.pdf>.
- Thaman, R. R. (2012). Wedelia (*Sphagneticola trilobata*) - Daisy invader of the Pacific Islands: The worst weed in the Pacific? Retrieved from http://webistem.com/psi2009/output_directory/cd1/Data/articles/000568.pdf.
- Tuomisto, H., Zuquim, G., & Cárdenas, G. (2014). Species richness and diversity along edaphic and climatic gradients in Amazonia. *Ecography*, 37, 1034–1046.
- Urrego, L. E., Bernal, G., & Polania, J. (2009). Comparison of pollen distribution patterns in surface sediments of a Colombian Caribbean mangrove with geomorphology and vegetation. *Review of Palaeobotany and Palynology*, 156, 358–375. <https://doi.org/10.1016/j.revpalbo.2009.04.004>
- van Roosmalen, M. G. M. (1985). *Fruits of the Guianan flora*. Utrecht-Wagenigen, The Netherlands: Institute of Systematic Botany, Utrecht University/Silvicultural Department of Wagenigen Agricultural University.
- van Soelen, E., Kim, J. H., Ventura Santos, R., Dantas, E. L., Vasconcelos de Almeida, F., Pinheiro Pires, J., ... Sinninghe Damsté, J. S. (2017).



- A 30 Ma history of the Amazon River inferred from terrigenous sediments and organic matter on the Ceará Rise. *Earth and Planetary Science Letters*, 474, 40–48. <https://doi.org/10.1016/j.epsl.2017.06.025>
- Vonhof, H. B., Wesselingh, F., Kaandorp, R. J. G., Davies, G. R., van Hinte, J. E., Guerrero, J., ... Ranzani, A. (2003). Paleogeography of Miocene western Amazonia: Isotopic composition of molluscan shells constrains the influence of marine incursions. *Geological Society of America Bulletin*, 115, 983–993. <https://doi.org/10.1130/B25058.1>
- Wassilieff, M. (2012). *Estuaries - Plants of the estuary*. Retrieved from <http://www.TeAra.govt.nz/en/estuaries/page-3>.
- Webb, S. D. (1995). Biological implications of the Middle Miocene Amazon seaway. *Science*, 269, 361–362. <https://doi.org/10.1126/science.269.5222.361>
- Wesselingh, F., Guerrero, J., Räsänen, M. E., Romero Pittman, L., & Vonhof, H. B. (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.
- Wesselingh, F. P., & Hoorn, C. (2011). Geological development of Amazon and Orinoco basins. In J. S. Albert & R. E. Reis (Eds.), *Historical biogeography of neotropical freshwater fishes* (pp. 59–67). Berkeley, CA: University of California Press.
- Wesselingh, F. P., & Ramos, M. I. F. (2010). Amazonian aquatic invertebrate faunas (Mollusca, Ostracoda) and their development over the past 30 million years. In C. Hoorn & F. P. Wesseling (Eds.), *Amazonia, landscape and species evolution: A look into the past* (pp. 302–316). Oxford, UK: Blackwell Publishing.
- Wesselingh, F., Räsänen, M. E., Irion, G., Vonhof, H. B., Kaandorp, R., Renema, W., ... Gingras, M. (2002). Lake Pebas: A palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainozoic Research*, 1, 35–81.
- Williamson, G. B., & Costa, F. (2000). Dispersal of Amazonian trees: Hydrochory in *Pentaclethra macroleoba*. *Biotropica*, 32, 548–552.
- Worts, G. F. (1958). *A brief appraisal of groundwater conditions and proposed program for water resources investigations in the coastal artesian basin of British Guiana*. Washington, DC: US Geological Survey.

SUPPORTING INFORMATION

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

How to cite this article: Bernal R, Bacon CD, Balslev H, et al. Could coastal plants in western Amazonia be relicts of past marine incursions?. *J Biogeogr*. 2019;46:1749–1759. <https://doi.org/10.1111/jbi.13560>