ORIGINAL ARTICLE

Amazon forest dynamics under changing abiotic conditions in the early Miocene (Colombian Amazonia)

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We dedicate this paper to the life and work of Gloria Galeano (1958–2016, Colombia), botanist and outstanding palm researcher.

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ABSTRACT

Aim We analysed in detail a past marine incursion event in north-western Amazonia and measured its effect on the forest composition. We also determined the sediment provenance in the fluvio-estuarine system and reconstructed the overall floral composition of the Amazon lowland forest during the Miocene climatic optimum.

Location A 60-m-thick sedimentary succession situated along the Caquetá River in Colombian Amazonia (0.77° S; 71.97° W).

Methods Palynological, geochemical and statistical analyses were performed on samples from organic-rich sediments.

Results The lower section was formed by fluvial floodplain deposits of Andean provenance rich in pollen of *Malvacipolloides maristellae* (aff. *Abutilon*) and *Rhoipites guianensis* (aff. *Vasivaea*). The middle section was formed by fluvial channel and estuarine swamp deposits of central Venezuelan provenance dominated by pollen of *Mauritiidites franciscoi* (*Mauritia*). Towards the top, the swamp deposits represent an estuarine floodplain with aquatic biomarkers, marine palynomorphs and mangrove pollen. The succession ended with fluvial floodplain deposits of central to southern Venezuelan origin with *R. guianensis* as dominant pollen type. Palynological diversity was high throughout the section with Andean- and Venezuelan-derived sediments each with their characteristic taxa. Tropical rain forest taxa, such as Arecaceae, Fabaceae, Sapotaceae, Malpighiaceae and Bombacoideae, were common in these sediments, although taxa adapted to drier conditions also occurred. We provide a 'figshare' link to an image library of selected taxa, as well as the raw counts and processed data.

Main conclusions The fluvio-estuarine system was of mixed origin with sediments and palynomorphs from the emerging Andes, but also from an area situated in the modern Orinoco Basin. Marine influence was linked to the Venezuelan source area and thus of indisputable Caribbean origin. Overall, a mixed forest with drought-resistant components existed in the drainage system during the Miocene climatic optimum. Our data provide a novel insight into the composition of the tropical lowland forest and the environments in north-western Amazonia prior to the main uplift of the central and northern Andes.

Keywords

Andean uplift, constrained hierarchical clustering, lipid biomarkers, marine incursion, *Mauritia* swamp, Miocene, non-metric multidimensional scaling, Orinoco, palynology, provenance

INTRODUCTION

The modern tropical rain forest in the Amazon region is becoming better known following multiple inventories of plant species and analysis of their ecological requirements (e.g. ter Steege *et al.*, 2013). However, to understand and predict biotic response to abiotic changes an improved knowledge of past sedimentary records on a long time-scale is required. The benefit of such information is that past rain forest composition can be viewed in the context of changing environmental conditions over thousands to millions of years. This approach has already led to debunking of the assumption that floral diversity dwindles in scenarios of global warming (e.g. Jaramillo & Cárdenas, 2013).

Long sedimentary records of Neogene age (23–2.5 Ma) can be found in the subsurface of the Amazon region but outcrops are rare. So far sparse core and outcrop studies in western Amazonia have provided an insight into the composition of the ancestral tropical lowland forest and its palaeoenvironmental setting (e.g. Hoorn, 1993; Wesselingh *et al.*, 2002; da Silva-Caminha *et al.*, 2010). Past response of plant assemblages to changing abiotic conditions are still poorly understood, and yet this knowledge is essential for the long-term evaluation of rain forest responses to environmental change.

Here, we revisit a sedimentary succession situated along the Caquetá River in Colombian Amazonia (Fig. 1a,b) that was deposited 17–16 Ma and has an excellent palynological record (Hoorn, 1994). The age coincides with the so-called middle Miocene climatic optimum (17–15 Ma), a period of much warmer climatic conditions than present (Zachos *et al.*, 2008). Moreover, the occurrence of strata with marine palynomorphs – in a succession otherwise characterized by tropical lowland taxa – implies changes from fresh water to oligohaline conditions (Hoorn, 1994; Boonstra *et al.*, 2015). The transition and the early Miocene age make this succession of particular interest for further study.

By applying a new combination of geochemical, palynological and statistical techniques (see also Appendix S1-S3 in Supporting Information) we aim to determine the provenance of these sediments and simultaneously follow the changes in palynological composition in an interval formed under marine influence. This analysis provides a more detailed reconstruction of the tropical lowland vegetation during the Miocene climatic optimum than currently available, and estimates the effects of changes in source areas, salinity and palaeoenvironment and their effect on the vegetation in the drainage basin.

Geographical and geological setting

The rivers in South America have a long history and are controlled by geological processes, climate and global sea level (Dunne & Mertes, 2007). During the Oligocene (34–23 Ma) the area of the modern Eastern Cordillera ceased to be a tropical lowland (< 1000 m) (Ochoa *et al.*, 2012),

and while progressive mountain building took place, sediment was transported into the sub-Andean foreland (Horton *et al.*, 2010) and (at least from Miocene onwards) into the Amazon region (Hoorn *et al.*, 1995; Roddaz *et al.*, 2005). To what extent this affected early Miocene river systems and their biota in western Amazonia is yet unknown.

Modern rivers in Amazonia are differentiated based on their source area, sediment load and water chemistry (Sioli, 1984) and have a rapid turnover (Salo *et al.*, 1986); continuous change is thus inherent to the Amazonian fluvial landscape. There are three distinct river types each with their characteristic floodplain environment and biota. Namely, white water rivers of Andean origin, black water rivers born in the tropical rain forest areas, and clear water rivers that originate in the crystalline rocks of the Guiana and Brazilian shields (Fig. 1c). Floodplains of Andean rivers (várzea) are, at the global scale, the most species rich, whereas forests on the floodplains of the Amazonian-born rivers (igapó) are much less species rich (Wittmann *et al.*, 2010; Montero *et al.*, 2014). A detailed description and classification of these wetlands can be found in Junk *et al.* (2011).

Our study site is situated along the Caquetá River, very near to the island of Mariñame (Hoorn, 1994) (Fig. 1a,b). The Caquetá River is of Andean origin, but has many Amazon-born tributaries, which resulted in a complex floodplain of levees, channel bars, swamps and terraces (Fig. 1b). At the Mariñame site, a 60 m sedimentary succession formed in a low sinuosity river system with its origins in Amazonia. Both the sediments and the depositional style suggest that this early Miocene river resembled the modern clear or black water rivers in Amazonia (Hoorn, 1994).

Fluvial deposits as records of past vegetation in western Amazonia

At least four Quaternary fluvial successions were documented along the Caquetá River, two of which lay close to our study site. These sections were previously studied to assess floodplain and vegetation dynamics following glacial–interglacial cycles (Urrego, 1997; Behling *et al.*, 1999; Giraldo *et al.*, 2008) (Fig. 1a,b) and present an excellent opportunity for a qualitative comparison between early Miocene and Quaternary sedimentary successions.

Palm pollen of *Euterpe/Genoma*, *Mauritia* and *Mauritiella* were abundant in the Quaternary sediments, together with Fabaceae, *Cecropia* and Moraceae/Urticaceae. Typically, the vegetation succession on the Caqueta River floodplain progressed from *Cecropia*-Moraceae/Urticaceae forests to *Mauritia* palm swamps with abundant Melastomataceae/Combretaceae and *Virola*. *Mauritia* swamps tended to occur on poorly drained soils that over time are either flooded again, or changed into the better drained *Euterpe/Genoma* floodplain forests (Urrego, 1997).

Wittmann *et al.* (2010) and Montero *et al.* (2014) described these successional stages as river 'abandonment',
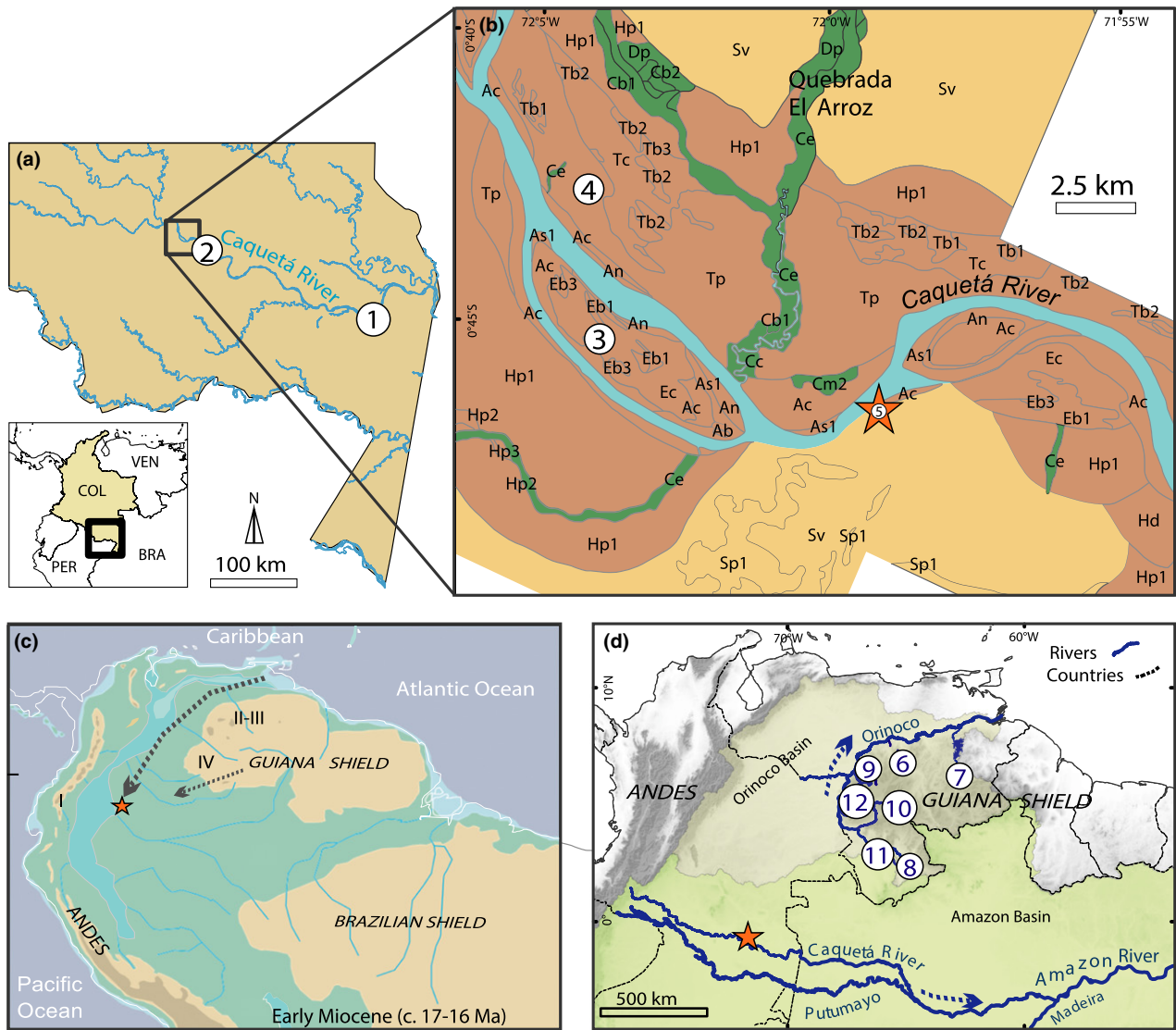
Figure 1 (a) The middle Caquetá region (Colombia, South America) and location of the study area (square), including the Holocene Manacaro (1) (Giraldo *et al.*, 2008) and Quinche (2) sections (Urrego, 1997); (b) Modern floodplain units near the Mariñame section illustrate the diversity of the landscape [modified after Duivenvoorden & Lips (1993) and digitized by E. Daza, Tropenbos Colombia]. (3) Isla Mariñame (Urrego, 1997) and (4) Pantano de Monica (Behling *et al.*, 1999), (5) Star = location of the composite Mariñame section. The main landscape units are: *ALLUVIAL PLAINS OF THE CAQUETÁ RIVER (dark brown): frequently inundated floodplains*: As1 = sand flats; An = natural levees; Ac = channel bar complex (poorly to well drained soils); *rarely inundated floodplain*: Eb1 and Eb3 = Backswamps (very poorly drained soils); *low terrace*: Tp = Flat, well drained parts; Tb1 and Tb2 = Low, poorly drained parts; *high terraces of the Caquetá River*: Hp1, Hp2, Hp3 = flat parts. *ALLUVIAL PLAIN OF AMAZONIAN RIVERS (green)*: Cb1 and Cb2 = Backswamps (poorly drained soil), Ce = high point bar complex, Dp = Terraces of Amazonian rivers (well drained soil). *TERTIARY SEDIMENTARY PLAINS (light brown)*: Sp1 = Flat parts; Sv = Plain with regular deep incision (well drained soils). (c) Palaeogeographical map of the early Miocene (modified after Hoorn *et al.*, 2010) with approximate location of the Mariñame section. The Proterozoic (> 541 Ma) Amazon Craton is subdivided into Guiana Shield in the north, and Brazilian Shield in the south. Sediment provenance: I = Andes; II, III – IV = NW Guiana Shield. The grey arrow indicates the hydrological flow direction during the early Miocene. (d) Present time geographical map with the main rivers in the Orinoco Basin that are mentioned in the text: (6) Cuchivero River, (7) Caroni River, (8) Upper Orinoco River, (9) Suapure River, (10) Ventuari River, (11) Pamino, Cunucunuma and Pasiba Rivers, (12) Parguaza and Sipapo Rivers. The blue arrows indicate the current flow direction of the rivers. Maps developed in ArcGIS® and ArcGIS 10.1™ software (Esri, 2012).

followed by swamp development and mature forest. They reported typical modern floodplain taxa such as *Alchornea*, *Alnus*, *Amanoa*, Asteraceae, Bombacoideae, *Borreria*, *Cecropia*, Cyatheaceae, Cyperaceae, *Casearia*, *Croton*, *Euterpe*, *Guarea*, *Hedyosmum*, *Ilex*, *Iriartea*, *Ludwigia*, Malpighiaceae, *Mauritia*, Melastomataceae/Combretaceae, *Macrolobium*, *Miconia*, Myrtaceae, *Podocarpus*, *Pouteria*, Poaceae, Polygalaceae, Rubiaceae, *Sapium*, Sapotaceae, *Virola* and *Vismia*

(see Appendix S2b in Supporting Information). This list formed a benchmark against which we compared the Miocene palynological assemblage.

MATERIALS AND METHODS

Data collection

Between 1988 and 1991 over 150 samples were collected at the Mariñame site of which 53 were studied, and their location in the section, lithology, sedimentary environment, provenance and type of analysis is listed in Table 1. The age for the succession is early Miocene based on biostratigraphy (17.7–16.1 Ma, T13-*Echitricolporites maristellae* zone, *sensu* Jaramillo *et al.*, 2011).

Sr-Nd isotopic composition and major and trace element concentration

Trace elements and Sr-Nd isotopic composition are good indicators of provenance and well-documented for western Amazonia (Fig. 2; Roddaz *et al.*, 2005). Elementary ratios (Cr/Th, Th/Sc) are also commonly used to determine the provenance of sediments (McLennan *et al.*, 1993). The preparation of sediments for Sr, Sm and Nd isotope analyses follow the procedures described by Gioia & Pimentel (2000) at the Geochronology Laboratory of the University of Brasilia. Further analytical details are available in Carignan *et al.* (2001). Concentrations for major and trace elements, and element ratios of selected samples, and interpretation of the data are given in Appendix S1a–d. We also evaluate the influence of sedimentary processes on the chemical composition of sediments, because sedimentary sorting can modify the concentrations of certain major and trace elements.

Bulk organic geochemical analyses

The bulk organic geochemical analysis of the samples provided us with the total organic carbon content (TOC), which is an indicator of the availability of organic matter in the depositional system. For this procedure, *c.* 0.3 g of crushed and homogenized sediment was decalcified by adding *c.* 35 mL of 4 M hydrochloric acid (HCl) and then shaken overnight (12 h), after which HCl was removed and the pH was neutralized by washing the sediments with ultra-pure distilled water. After freeze-drying, the samples were re-weighed. An elemental analyser (Flash EA 1112 series) was used to determine the TOC relative to weight (wt%) and the stable carbon isotopic composition of TOC ($\delta^{13}C_{TOC}$). Analyses were determined at least in duplicate and the analytical error was on average better than 5%. Isotope values were calibrated to a benzoic acid standard [$\delta^{13}C_{TOC} = -28.1‰$ with respect to Vienna Pee Dee Belemnite (VPDB) calibrated on NBS-22]. The analytical error was usually smaller than ± 0.15‰ for $\delta^{13}C_{TOC}$ (Fig. 3a).

Lipid biomarker analysis

Lipid biomarkers are also indicators of provenance and, more specifically, can link organic matter sources to the marine or terrestrial environment. Thirty freeze-dried and homogenized samples (0.5 and 12 g) were extracted using an ultrasonic water bath. Glycerol dialkyl glycerol tetraethers (GDGTs) were analysed in the polar fraction of the extract using liquid chromatography coupled with mass spectrometry using conditions previously described (Schouten *et al.*, 2007). For quantification purposes, a fixed amount of an internal GDGT standard was added. A ratio between branched and isoprenoid GDGTs and crenarchaeol, the branched and isoprenoid tetraether (BIT) index, provides information on the relative contribution of fresh water aquatic *in situ* versus soil-derived GDGTs (Hopmans *et al.*, 2004) (Fig. 3a).

Palynological analysis

Sporomorphs (pollen and spores) are good indicators of past plant composition, whereas palynomorphs, such as dinocysts and microforaminifers, are indicative of marine influence. Forty-three palynological samples from the Mariñame section were previously analysed by Hoorn (1994), and nine additional samples were newly processed and analysed to increase the resolution of the fluvial to estuarine transition. All samples with counts below 100 were excluded leaving a total of 47 with a pollen sum of around 300 and in total 325 different morphological types. The processing method followed Hoorn (1993) and identifications were made using the online Pollen Morphological Database (Jaramillo & Rueda, 2008) and diverse literature.

Sporomorph concentration was calculated for all samples based on the *Lycopodium* tracer added per measured volume of sediment sample (1 tablet to 1 or 1.5 cm³ sediment), concentrations of selected taxa can be found in Appendix S2a. Diagrams were made with TILIA 7.6 software (Grimm, 1991). Botanical affinities and ecological conditions follow Lindeman (1953), Lorente (1986), Hoorn (1993, 1994), Jaramillo *et al.* (2011), and pers. comm. by Giovanni Bogota-Angel, Antoine Cleef and Florian Wittmann (see Appendix S2b). Lithology, depositional environment, palynological groups, sporomorph concentration, and pollen and palaeoenvironmental zones are shown in Fig. 3b (and see Appendix S2c). An image library of selected taxa, and the raw counts and processed data are available under: https://figshare.com/s/1b9d7888f59211e4833506ec4bbcf141.

Multivariate analysis

Non-metric multidimensional scaling (NMDS) (Fig. 4) and constrained hierarchical clustering, including the agglomeration method 'CONISS' (maintaining the stratigraphic position of the samples) (Appendix S3b), were applied to synthesize hundreds of sporomorph types and to group

Table 1 Relation between samples, depth in section, lithology, analytical techniques and environmental zones in the Mariñame section, Colombia, South America. nMDS-based zones are based on the original data set and slightly diverge due to the lower sample number (see Appendix S3b; Hoorn, 1994). Samples in bold are newly counted samples, added for pollen resolution and excluded from statistical analysis.

Mariñame composite section

Depth (m)	Lithology	Marine palynomorphs (Hoorn, 1994; Boonstra et al., 2015)	Samples	Geochemistry	Palynology	Statistical analysis	nMDS	Pollen zones	Environment	Provenance
49.75	Very sandy brown clay/sand lenses/bioturbation		Mar 17-91	X	X	X	40	Zone IV	Fluvial floodplain	Pamoni, Cunucunuma, Pasiba rivers (Fig. 1d, 11)
49.65	Very sandy brown clay/sand lenses/bioturbation		**Mar 16-91**		X					
49.55	Very sandy brown clay/sand lenses/bioturbation		Mar 15-91	X	X	X	39			
49.45	Very sandy brown clay/sand lenses/bioturbation		**Mar 14-91**		X					
49.35	very sandy brown clay/sand lenses/bioturbation		Mar 13-91	X	X	X	38			
49.25	Pyrite level/botanical remains/very sandy	1 foram	**Mar 12-91**		X					
49.15	Very sandy brown clay/sand lenses/bioturbation		Mar 11-91	X	X	X	37			
49.05	Very sandy brown clay/sand lenses/bioturbation		**Mar 10-91**		X					
48.95	Light grey clay; bioturbation	9 forams; 8 dinos	Mar 9-91	X	X	X	36	Zone III	Estuarine floodplain	Cuchivero & Caroni rivers (Fig. 1d, 6, 7)
48.5	Light grey clay		Mar 8-91		<100 pollen	X	35			
47.9	Light grey clay	5 forams	Mar 7-91	X	X	X	34			
47.6	Light grey clay		Mar 6-91		X	X	33			
47.2	Sandy light grey clay	2 forams; 27 dinos	Mar 5-91	X	X	X	32			
47.1	Light grey clay, sand lenses	14 forams	Mar 3-91	X	X	X	31			
47	Dark grey clay/sand lenses	31 forams	Mar 2-91	X	<100 pollen	X	30			
46.9	Dark grey clay/sand lenses	24 forams	Mar 1-91	X	<100 pollen	X				
46.8	Very sandy light grey clay	61 forams	3 Is 138	X	X	X	29			
46.7	Sandy lignite	8 forams	3 Is 137	X	X	X	28			
46.6	Sandy lignite		**3 Is 136**		X	X	27	Zone II	Estuarine swamp	Cuchivero & Caroni rivers (Fig. 1d, 6, 7)
46.5	Very fine sand/1–2 mm thick laminae	1 foram	3 Is 135	X	X	X	26			
46.4	Sandy lignite/white fragments		3 Is 134	X	X	X	25			
46.3	Lignite/very fine sand/lenses 0.2–0.5 mm	1 foram	3 Is 133	X	X	X	24			
46	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 130	X	X	X				
45.8	Lignite/very fine sand/lenses 0.2–0.5 mm		**3 Is 128**		X					
45.5	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 125	X	X	X	23			
45.3	Lignite/very fine sand/lenses 0.2–0.5 mm		**3 Is 123**		X					
45	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Isl 120	X	<100 pollen					
44.8	Lignite/very fine sand/lenses 0.2–0.5 mm		**3 Is 118**		X					
44.5	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 115	X	X	X	22			
44.2	Lignite/very fine sand/lenses 0.2–0.5 mm		**3 is 112**		X					
44	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 108	X	X	X	21			
43.6	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 104	X	X	X	20			

Table 1 Continued

Mariname composite section

Depth (m)	Lithology	Marine palynomorphs (Hoorn, 1994; Boonstra et al., 2015)	Samples	Geochemistry	Palynology	Statistical analysis	nMDS	Pollen zones	Environment	Provenance
43.2	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 100	X	X	X	19			
42.7	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 95	X	X	X	18			
42.2	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 90	X	X	X	17			
41.8	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 86	X	X	X	16			
41.2	Lignite/very fine sand/lenses 0.2–0.5 mm		3 Is 82	X	X	X	15			
40.8	Lignite/very fine sand/lenses 0.2–0.5 mm		Mar_10		X	X	14			
40.4	lignite/very fine sand/lenses 0.2–0.5 mm		Mar_6		X	X	13			
40	Lignite/very fine sand/lenses 0.2–0.5 mm		Mar_3		X	X	12			
17.3	Fine sand/coffee brown clay		Mar_33	X				Zone I	Fluvial floodplain	sub-Andean zone & Madeira River (Fig. 1d)
17.1	Silt/brown-grey Clay/coal fragments		Mar_32	X	X	X	11			
16.9	Silt/brown-grey clay/coal fragments		Mar_31		X	X	10			
16.7	Silt/brown-grey clay/coal fragments		Mar_30		X	X	9			
16.5	Silt/brown-grey clay/coal fragments		Mar_29		X	X	8			
16.3	Silt/brown-grey clay/coal fragments		Mar_28	X	<100 pollen					
4.5	Very sandy cream clay/coal fragments		Mar_40		X	X	7			
4.4	Very sandy cream clay/coal fragments		Mar_39		X	X	6			
4.3	Silt/coffee brown clay		Mar_38		X	X	5			
4.1	Silt/coffee brown clay		Mar_37	X	X	X	4			
3.9	Silt/coffee brown clay		Mar_36		X	X	3			
3.7	Silt/coffee brown clay		Mar_35		X	X	2			
3.5	Fine sand/coffee brown clay		Mar_34		X	X	1			

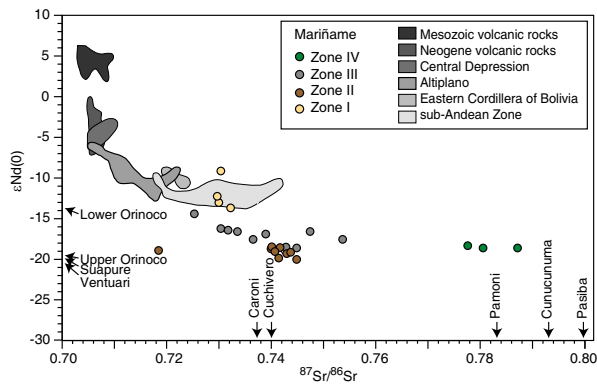**Figure 2** $^{87}Sr/^{86}Sr$ vs. $\varepsilon_{Nd(0)}$ cross-plot showing provenance for Mariñame (Colombia, South America) sediments; colours are in agreement with corresponding pollen zone. Values of source areas in western Amazonia are following Roddaz *et al.* (2005), and isotopic composition from Solimões and Madeira rivers following Viers *et al.* (2008). Black arrows indicate $^{87}Sr/^{86}Sr$ values (Palmer & Edmond, 1992) and $\varepsilon_{Nd(0)}$ values (Goldstein *et al.*, 1997) in different rivers of the Orinoco Basin.

stratigraphically adjacent samples. We detected associations of samples of similar composition and hypothesized how the pollen assemblage changed over time (see Appendix S3a,b). The result of the constrained hierarchical clustering was used as input to obtain a vegetation table (*sensu* Mueller-Dombois & Ellenberg, 1974), and to summarize all taxa into five distinct palynological groups (Fig. 3b; Appendix S3c).

All analyses were carried out in R (R Core Team, 2015). Appendix S3 provides a detailed account of all statistical methods and intermediate results. A subset of the original data from Hoorn (1994) was used for this analysis, and consisted of 137 taxa and 40 samples; raw counts were standardized by Wisconsin double standardization. Next a dissimilarity matrix was obtained, using the Horn-Morisita index (Horn, 1966) and this was used as input for the NMDS. A combined table includes the distance matrix (see Appendix S3a; part 1), NMDS (see Appendix S3a; part 2) and weighted average of the taxa (see Appendix S3a; part 3). In addition, the specificity of taxa to each of the four palynological zones was established through a contingency table, which is represented by a Venn diagram (see Appendix S3d, e). An estimate of the changes in pollen diversity is shown in a curve of expected taxa richness throughout the four pollen zones (see Appendix S3f) and finally a bubble-plot summarizes the most abundant taxa in the pollen register (see Appendix S3g).

RESULTS

The Sr and Nd isotopes in the organic-rich sediment layers at the Mariñame site suggest a mixed origin, with the lower part of the section being of Andean provenance, and the upper part of the section of Venezuelan, cratonic, source (Fig. 2). All geochemical results are compared with the palynological data (Fig. 3a,b) and suggest a relationship between

abiotic and biotic changes; this is also confirmed by the NMDS ordination (Fig. 4), which shows environmentally related samples [four different colours in panel (a) and their characteristic taxa (panel b)]. Moreover, sediments in the upper section have a marine component, which suggests that the marine influence was of Caribbean origin.

Isotope tracers point to a mixed source for the early Miocene Amazon sedimentary system

Provenance varies throughout the section as is shown in Fig. 2, where $^{87}Sr/^{86}Sr$ vs. $\varepsilon Nd(0)$ values of the sediments are compared with relevant source fields.

Zone I

Overall, Sr and Nd isotope ratios and Nd-model ages of sediments from this zone have a younger sediment source than those of zones II to IV (see Appendix S1c). In zone I, the Sr isotope ratios range between 0.730 and 0.732, while $\varepsilon_{Nd(0)}$ values range between −9.3 and −13.8, and the Nd-model ages range between 1.65 and 2.04 Ga. The isotopic composition of these sediments is comparable with values found in sediments from the sub-Andean basins (Roddaz *et al.*, 2005) and suspended material of the Madeira River (Fig. 1d) (Viers *et al.*, 2008). Therefore, sediments of zone I are likely to be of Andean origin (Fig. 1c, I).

Zones II and III

The Sr isotope ratios in these zones range between 0.719 and 0.754 and the $\varepsilon_{Nd(0)}$ values range between −14.5 and −20.0. The Nd-model ages indicate that the sources of these sediments have an average age between 1.75 and 2.27 Ga. Within these zones, sediments with marine palynomorphs account for most of the scatter in Fig. 2. For example, samples from zones II and III that exhibit no indications of marine influence have $^{87}Sr/^{86}Sr$ values ranging between 0.740 and 0.745 and $\varepsilon_{Nd(0)}$ values between −18.7 and −20. These Sr-Nd isotopic compositions indicate that the Guiana or Brazilian shields were important source areas of these sediments (Fig. 1c). Dissolved Sr isotopes of tributaries of the modern Orinoco River that drain rocks of the Guiana Shield, such as the Cuchivero River ($^{87}Sr/^{86}Sr = 0.737–0.744$) (Fig. 1d, 6) and the Caroni River ($^{87}Sr/^{86}Sr = 0.732–0.742$) (Palmer & Edmond, 1992) (Fig. 1d, 7), have isotope ratios comparable with those observed in the Mariñame samples. The reported $\varepsilon_{Nd(0)}$ values in the Orinoco Basin are also comparable with values around 0.5116 for the upper Orinoco, Suapure and Ventuari rivers (Fig. 1d, 8–10) (Goldstein *et al.*, 1997) corresponding approximately to $\varepsilon_{Nd(0)} = −20$.

Zone IV

This zone is characterized by the highest radiogenic Sr isotope values (0.710–0.787) within the whole succession. Similar to

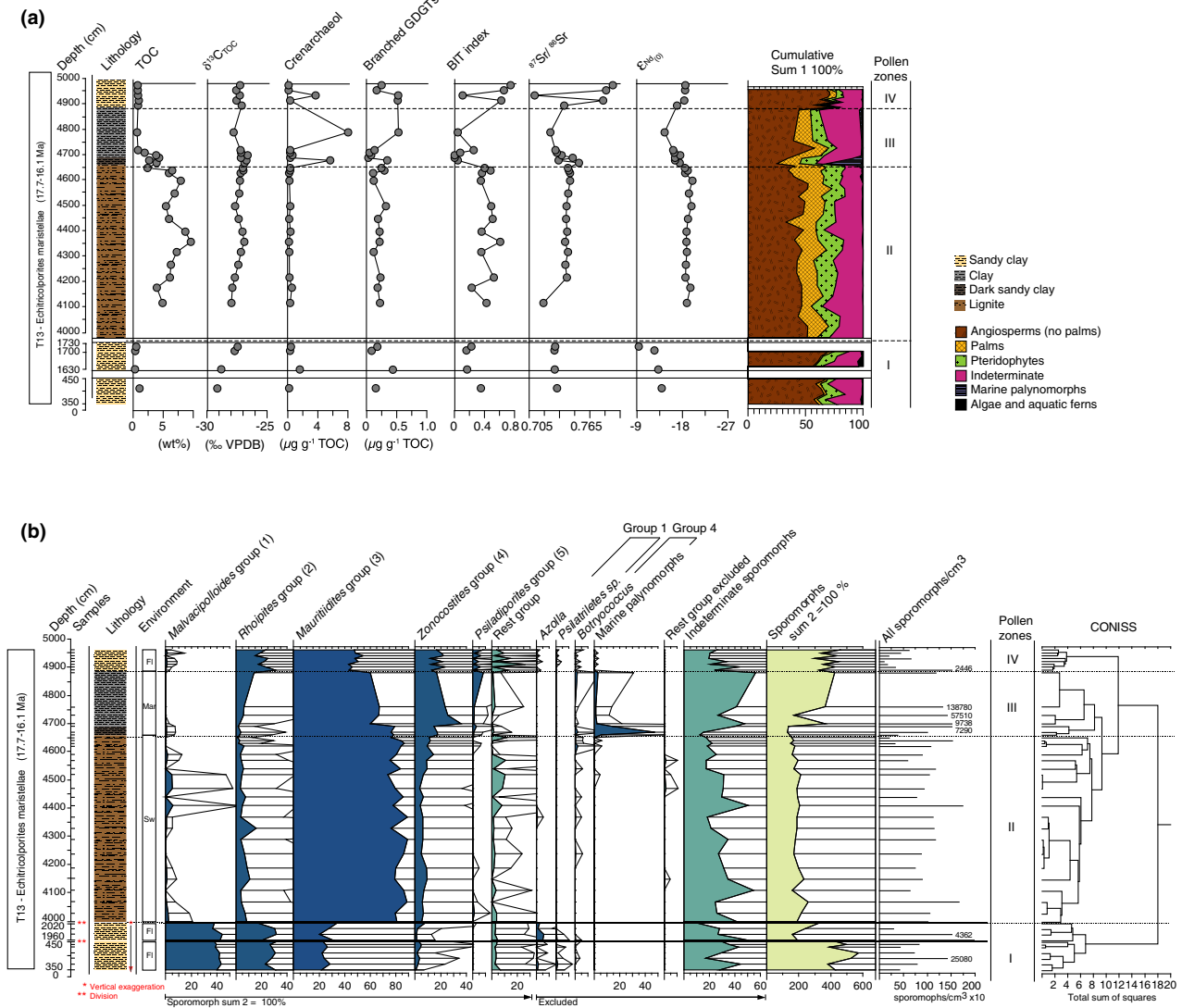**Mariñame Composite Section**

(a)

(b)

Figure 3 (a) Overview diagram of biomarkers including total organic carbon (TOC), branched and isoprenoid tetraether (BIT) index, and provenance indicators ($\varepsilon_{Nd(0)}$, $^{87}Sr/^{86}Sr$) in Mariñame (Colombia) section. On the far right is a palynological cumulative diagram (pollen sum 1), and zonation based on geochemical and palynological data (see also Appendix S1-S2). Pollen sum 1 includes: all angiosperms, all pteridophytes, algae and aquatic ferns, marine palynomorphs, and indeterminate sporomorphs. (b) Palynological summary diagram of Mariñame section with zones based on CONISS in TILIA 7.6 software (Grimm, 1987) (detailed diagram in S2c). The diagram is constructed on pollen (sporomorph) sum 2, which includes angiosperm and pteridophyte taxa.

the sediments from zones II and III, Sr isotopes of these sediments are also consistent with a cratonic sediment source. Parts of the modern Orinoco Basin also have very high Sr ratios as revealed by modern day rivers Pamoni ($^{87}Sr/^{86}Sr = 0.783$), Cunucunuma ($^{87}Sr/^{86}Sr = 0.793$) and Pasiba ($^{87}Sr/^{86}Sr = 0.799$) (Palmer & Edmond, 1992) (Fig. 1d, 11), which are comparable with the values observed in samples from zone IV. Even more radiogenic Sr values have been found in drainages on the western side of the Guiana Shield, for example in the Parguaza River ($^{87}Sr/^{86}Sr = 0.819–0.854$) and Sipapo River ($^{87}Sr/^{86}Sr = 0.910–0.922$) (Palmer & Edmond, 1992) (Fig. 1d, 12). The south to middle part of the Guiana Shield therefore is a likely sediment source (Fig. 1c. Area IV).

Some samples of Mariñame zones III and IV have high Zr/Sc ratio and enrichment in heavy REE over light REE that could be due to zircon accumulation caused by sedimentary sorting (see Appendix S1d). However, the Al/Si ratios, which can be considered as a proxy for Amazon sediment grain size (Bouchez et al., 2011), show no correlations with Zr and Hf and elemental ratios and isotopic ratios suggesting that sedimentary sorting did not affect the geochemistry of analysed sediments.

Chemical weathering can also modify the geochemistry of the sediments. Such modification could be the case for the Nd isotopic composition that shows negative correlation with the Chemical Index of Alteration (CIA) values (see Appendix S1d). However, the absence of any correlation of the CIA values with other provenance indicators (Sr isotopes,
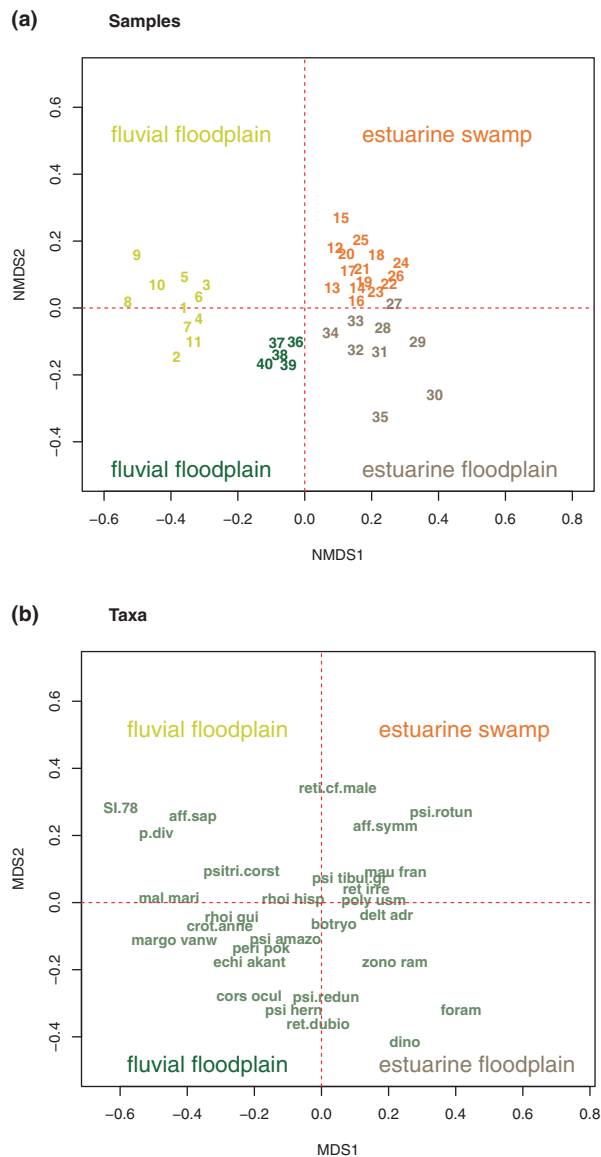
(a)

(b)

Figure 4 (a) nMDS ordination plot of 40 palynological samples from the Mariñame composite section and (b) a selection of the most characteristic taxa (from a total of 137) after filtering out singletons and doubletons. The abbreviations are explained in Appendix S3a (part 3). The main pollen assemblages are along two optimal dimensions. Left upper quadrant: oldest fluvial floodplain (pollen zone I). Right upper quadrant: estuarine swamp (pollen zone II). Bottom left: youngest fluvial floodplain (pollen zone IV). Bottom right: estuarine floodplain (pollen zone III).

Eu/Eu*, Cr/Th, Th/Sc) instead suggests that post-depositional chemical weathering did not control the chemical composition of the sediments.

Biomarkers as indicators of changing aquatic conditions

Lipid biomarkers are chemical relicts of organisms, and derive from plants, algae and bacteria. GDGTs and crenar-

chaeol are a specific group of lipids that are produced in soils and in aquatic environments. Their relative distribution in sediments can be used as a tool to reconstruct past environmental conditions. Studies carried out in the central Amazon drainage basin showed that in the modern Amazon River system crenarchaeol is mainly produced in the aquatic (lake/river) system, with relatively low amounts in soils (Kim *et al.*, 2012; Zell *et al.*, 2013a,b).

Both crenarchaeol and branched GDGTs are found in all Mariñame samples in varying concentrations. TOC content varies between 0.3 and 10wt% and $\delta^{13}C_{TOC}$ between -27 and $-29‰$, with no major shift through time (Fig. 3a). The BIT index in the Mariñame section varies between 0.0 and 0.7 (Fig. 3a). Shifts in the BIT index may be a consequence of changes in concentration of either branched or isoprenoid GDGTs. Summed concentrations of the branched GDGTs vary only from 0.1 to 0.5 µg g^{-1} TOC, whereas the concentration of crenarchaeol varies much more, that is, between 0.1 and 8.0 µg g^{-1} (Fig. 3a). Crenarchaeol concentrations are substantially higher in zone III, resulting in reduced values of the BIT index (Fig. 3a). Interestingly, the changes in biomarker composition in these strata coincide with the occurrence of marine palynomorphs (Fig. 3b). Cumulatively the pollen and BIT index data indicate a relatively lower input of organic debris from terrestrial vegetation, suggesting an increase in water level in the estuarine floodplain.

Palynological change at the transition from fluvial towards estuarine conditions

The Mariñame section was subdivided into the following four palynological zones (Fig. 3b; see Appendix S2c, S3b-c):

Zone I

The lithology is characterized by light brown clays. Most conspicuous in this zone are *Malvacipolloides maristellae* (formerly *Echitricolporites maristellae;* aff. *Abutilon*) and *Magnastriatites grandiosus (Ceratopteris)*, which virtually disappear in zones II to IV. The latter is an aquatic floating fern and together with *Azolla* is indicative open water conditions. The occurrence of *Echiperiporites akanthos (Sagittaria)* further underscores the waterlogged conditions of the floodplain environment. Other common taxa are *Rhoipites guianensis* (aff. *Vasivaea*), *Ranunculacidites operculatus (Alchornea)*, *Perisyncolporites pokornyi* (Malpighiaceae), *Psilastephanocolporites matapiorum* (Sapotaceae?), *Crassiectoapertites columbianus* (Fabaceae) and *Retitricolporites crassicostatus* (Rubiaceae). The co-occurrence of *R. guianensis* with *E. akanthos, Corsinipollinites oculuscnoctis (Ludwigia)* and *Monoporopollenites annulatus* (Poaceae), suggests locally wet conditions that are in agreement with floodplain conditions. Instead, the presence of Polygonaceae (species undefined) could point at a semi-terrestrial, herbaceous to shrubby undergrowth (if of *Rumex, Coccoloba, Triplaris* affinity) or – more likely – further support the swampy nature of the environment (if of *Persicaria* affinity). Taxa such as

Mauritiidites franciscoi (*Mauritia*), Polygalaceae, *Perfotricolpites digitatus* (*Merremia*) and aff. *Protium* also occur in this zone and are presently found in the riparian habitat and/or on *terra firme*. These Andes-derived freshwater floodplain deposits differ from other deposits in the section by the predominance of group 1 and 2 sporomorphs, and the exclusive occurrence of 22 (out of 137) sporomorphs (see Appendix S3d,e).

Zone II

Sandy lignites with pyrite nodules and brown clays form the upper half of the section, and they mark the onset of estuarine conditions. *Mauritiidites franciscoi*, predominates in this zone and is mainly accompanied by Polypodiaceae such as the *Laevigatosporites tibuensis* and *Verrucatosporites usmensis* groups, and *Heterocolpites incomptus* (*Miconia*, Melastomataceae-Combretaceae), *Retitrescolpites? irregularis* (*Amanoa*, Euphorbiaceae), *Retitricolpites caquetanus* (*Catostemma*), *Psilatricolpites exiguus* (*Dalbergia*) and *Deltoidospora adriennis* (*Acrostichum aureum*). The latter is a fern that nowadays grows near mangroves (Lindeman, 1953; van Andel, 2003).

Zone III

The clays and very sandy clays and lignites in this part of the section are characterized by marine palynomorphs, the mangrove taxon *Zonocostites ramonae* (*Rhizophora*) and its associates *Retitricolpites depressus*, *R. caputoi*, and *Psilastephanocolporites schneiderii* (*Tournefortia maculate*, Boraginaceae), and the rise of aquatic biomarkers (Fig. 3a, BIT index). *Mauritiidites franciscoi* is still abundant, but another common palm on this estuarine floodplain is *Psilamonocolpites nanus* (aff. *Euterpe*), which currently is characteristic for environments at the interface of brackish and fresh water (van Andel, 2003; pers. comm. F. Wittmann). Taxa such *Psilatricolpites papilioniformis*, *Heterocolpites rotundus* (Melastomataceae), *Azolla*, *Psilatricolporites* spp. (Sapotaceae), *Retitricolporites solimoensis* and *Bombacacidites baumfalkii* (Bombacoideae) all become rarer or completely disappear in zone III, suggesting that they were affected by the increase in saline water. The estuarine floodplain has no exclusive taxa of its own, but shares four with the estuarine swamp [*R. depressus*, *Retitriporites* sp. (*Duroia*), *Gemmatricolpites pulcher* and *Psilabrevitricolpites rotundus*] (see Appendix S3d,e).

Zone IV

The upper fluvial floodplain is formed of sandy brown clays and immediately overlies the estuarine floodplain (zone III). It is characterized by the abundance of *Rhoipites guianensis*, a drop in marine palynomorphs, *Zonocostites ramonae* (*Rhizophora*), and *Mauritiidites franciscoi* (*Mauritia*), and the presence of *Psiladiporites redundantis* and associated taxa. Other taxa such as *Syncolporites* cf. *incomptus* (Loranthaceae?) and *Psilastephanoporites herngreenii* (Apocynaceae) are exclusive to this zone.

Seemingly, plant taxa such as *Rhoipites guianensis*, *Ranunculacidites operculatus*, *Perisyncolporites pokornyi*, *Crassiectoapertites columbianus* and *Retitricolporites crassicostatus* (among others) are sensitive to increased salinity, but impervious to changes in sediment provenance. These taxa and their associates are mostly restricted to the Andean and the cratonic floodplain sediments of zone I and IV. Other taxa are distinctly provenance sensitive, with one-third of taxa being either exclusive to the Venezuelan or the Andean sediment type (see Appendix S3d,e). Another 46 taxa occur throughout the section, suggesting they are neither sensitive to provenance nor salinity changes (see Appendix S3d,e). This makes us suspect that a significant portion of the total assemblage was formed by generalist plants, able to adapt in the wide arrange of environmental settings.

Rarefied palynological diversity in our samples (expected species richness in random subsamples of 150) was high and − on average − did not vary much throughout the section (see Appendix S3f). Although it is difficult to make assertions about diversity based on a relative small subsample size, it should be noted that our estimate is conservative as many singletons were grouped as 'indeterminate'. A drop in diversity occurs between the lower fluvial floodplain (zone I) and the estuarine swamp (zone II), and a somewhat lower average remains throughout the estuarine floodplain (zone III), coinciding with an increase in pollen concentration. In the upper fluvial floodplain (zone IV), when marine influence fades, the diversity increases again showing values similar to pollen zone I. This decline in diversity coincides with the predominance of *Mauritia*, a palm known to occur in single-species stands, it is thus likely that the drop in pollen diversity is local artefact rather than representative of a regional change in forest composition (see Appendix S3f).

The scattered presence of *Podocarpidites* sp. (*Podocarpus*) throughout the section underscores the long-term presence of this taxon in the region, and its tolerance to high temperatures and poor edaphic conditions (Behling *et al.*, 1999). The presence of Polygonaceae, Myrtaceae, Sapotaceae and *Stephanocolpites* spp. (aff. *Borreria*) together with *Psilatricolporites costatus* (*Casearia*? Salicaceae) and *Margocolporites vanwijhei* (Fabaceae, Caesalpinioideae) are consistent with mesic fluvial systems. This, and the abundance of taxa with affinity to *Abutilon*, *Vasivaea* and Fabaceae, all are suggestive for somewhat dryer conditions than at Present.

Many taxa documented in the Miocene section coincide with taxa present in the modern floodplains of western Amazonia, but there are also notable exceptions such as *Rhoipites guianensis* and *Malvacipolloides maristellae*. The latter two are exclusive to the Miocene (and older records in the case of *R. guianensis*), whereas taxa such as *Alnus*, Asteraceae, *Cecropia* (and possibly *Iriartea*), either arrived or evolved at a later stage in northern South America. Furthermore, from our list of palynological hyperdominants at least *Mauritiidites franciscoi* (*Mauritia*) and *Psilamonocolpites amazonicus* and *P. nanus* (cf. *Euterpe*) have the same status as in the modern forest (ter Steege *et al.*, 2013) (see Appendix S3g).

DISCUSSION

The combined effect of climate, provenance and sedimentary processes on past plant composition can be difficult to untangle. In a fluvial system, the interaction of the different controlling factors is inherent to the system and produces a palynological record that represents both local plants and those growing upstream in the river source area. In our study, we combined palynological and geochemical analyses, and applied multivariate techniques to get a better understanding of the relation between sediment source, depositional environment, and the overarching effect of climate on both local and regional vegetation composition.

Throughout the Mariñame sedimentary record there is considerable variation both in sediment and species composition. Our data suggest that this variation is due to: (1) a mixed sediment provenance, mostly from the Guiana Shield in Venezuela and to a lesser degree from the Andes, and (2) a change from fresh water to oligohaline conditions. Palynological diversity does not significantly vary throughout the section, but changes in composition do occur and mainly are provenance-dependent, whereas marine influence neither dramatically alters the composition nor the palynological diversity. This knowledge enhances our understanding of the early Miocene sedimentary and biotic system in north-western Amazonia. Nevertheless, it remains difficult to interpret accurately the precise local response of the forest to changes in salinity and provenance.

The abundance of *Rhoipites guianensis* (aff. *Vasivaea*) and *Malvacipolloides maristellae* (aff. *Abutilon*) in zones I and IV is one of the most distinct features of our palynological record. These taxa are also known from other early Miocene records in northern South America (e.g. Germeraad *et al.*, 1968; Dueñas, 1980; Lorente, 1986; Hoorn, 1993; Rull, 2001; Jaramillo *et al.*, 2011) and their absence in Quaternary fluvial records and the modern várzea and igapó (e.g. Urrego, 1997; Behling *et al.*, 1999; Giraldo *et al.*, 2008; Wittmann *et al.*, 2010) suggests fundamentally different conditions in the early Miocene lowlands. We hypothesize that these taxa are of Gondwanan origin and, together with taxa consistent with white sands and rocky outcrops and the woody savannas of *Campinas, Cerrados* and *Caatingas,* point to more pronounced dry seasons and increased seasonality during the early Miocene. This scenario would fit well in the current palaeogeographical model where the Andes orographic barrier is incomplete until the middle Miocene inducing less precipitation eastwards of the Andes (Hoorn *et al.*, 2010; Barnes *et al.*, 2012).

Rhoipites guianensis and *Malvacipolloides maristellae* both disappear at the onset of estuarine conditions in zone II with only *R. guianensis* returning in zone IV. The permanent absence of *M. maristellae* in zones II to IV can be interpreted either as being linked to the Andean sediment source, or to the marine influence. Notably, in the early Miocene of Venezuela *M. maristellae* (or *Echitricolporites maristellae*, as it is referred there) is rare or absent in sediments with marine palynomorphs and predominates when there are no marine indicators (Lorente, 1986; Rull, 2001). This observation leads us to believe that *M. maristellae* is, similar to *R. guianensis*, salinity sensitive. In the light of this inference, the association of both taxa with a selection of other sporomorphs exclusive to zone I is more likely to be related to the prevailing fresh water conditions rather than the Andean sediment source.

The predominance of *Mauritiidites franciscoi* and its associated taxa in zones II to III of the Miocene record do resemble the palynological composition of the Quaternary *Mauritia* swamp successions in north-western Amazonia (Urrego, 1997; Behling *et al.*, 1999; Giraldo *et al.*, 2008) and in Venezuela (e.g. Leal *et al.*, 2011). This assemblage also is reminiscent of the modern *morichales* (*Mauritia* stands in Orinoquia), *canaguchales* (*Mauritia* stands in Amazonia), and the Venezuelan highlands (see Lasso *et al.*, 2013). However, diagnostic taxa of the coastal plain and estuaries, such as marine palynomorphs and mangrove pollen, do not occur in the modern floodplain vegetation in central and western Amazonia nor in its Quaternary palynological records. Yet marine palynomorphs are associated with *Mauritia* in our Miocene record. This finding suggests that upper coastal plain mangroves and *Mauritia* palm back-swamps of the Atlantic seaboard is an approximate analogue to the swamp and floodplain deposits of zones II and III. In these settings mangroves such as *Rhizophora* are typical in both modern vegetation and the Quaternary palynological records (Lindeman, 1953; Behling *et al.*, 2001; van Andel, 2003; Urrego *et al.*, 2009). This coastal influence makes the palynological assemblage of zone III, together with the Venezuelan provenance of the sediments, a convincing indicator of past marine influence of Caribbean origin in north-western Amazonia as proposed in Hoorn (1993) and Boonstra *et al.* (2015).

CONCLUSIONS

Our cross-disciplinary study of an early Miocene sedimentary succession in north-western Amazonia provided us with new insights concerning the sediment source and plant composition of this system. Sediments mainly originated in the Venezuelan Guiana Shield, but also had an Andean component. Moreover, the organic-rich sediments of Venezuelan origin contain marine palynomorphs and pollen, which are indicative of coastal conditions. This reinforces the notion that the early Miocene marine influence in north-western Amazonia was of Caribbean origin. Intriguingly, the drainage of the fluvio-estuarine system flowed in opposite direction to that of the modern Orinoco.

The low salinity levels in the estuarine environment seemingly did not dramatically alter the overall lowland forest diversity, but caused changes in composition. Additionally, the overall palynological composition and diversity of this early Miocene fluvio-estuarine system points at a mixed forest with drought-resistant floodplain forest taxa. Viewed in a deep time perspective, we conclude that the Miocene lowland forest must have been a floristically diverse and dynamic

ecosystem with characteristic components of taxa that nowadays are rare or non-existent, and possibly of Gondwanan origin. Our record illustrates the nature and resilience of the lowland forest to abiotic change in the globally warmer world of the Miocene.

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SUPPORTING INFORMATION

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

Appendix S1 Geochemistry (S1a–d).
Appendix S2 Palynology (S2a–c).
Appendix S3 Multivariate analysis (S3a–g).

BIOSKETCHES

This project was developed in the context of the CLIM-AMAZON programme, the joint Brazilian-European facility for climate and geodynamic research on the Amazon River Basin sediment under the European Union's Seventh Framework Program. **Sonia Salamanca Villegas** is specialized in vegetation dynamics and statistical analysis of large data sets. In 1985, she was part of the Tropenbos International expedition that designated the study area in Colombian Amazonia. **Els van Soelen** is geologist with a special interest in (organic) geochemistry. **Milan Teunissen van Manen** did this research as part of her MSc thesis. **Carina Hoorn** is geologist/palynologist with a never-ending interest in the natural history of Amazonia. Her research focus is landscape changes in Amazonia through deep time.

Author contributions: C.H., S.S.V. and J.H.K. made the research plan; M.T.M., E.S., S.S.V. and C.H. collected and analysed the data; S.G.A.F. made the maps and contributed to the writing; E.L., R.V.S., M.R., E.L.D., J.S.D. and J.H.K. all contributed to the analysis and made improvements to the manuscript; C.H. directed this study and led the writing.

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