Late Quaternary landscape evolution of northeastern Amazonia from pollen and diatom records

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ABSTRACT

The main goal of this study was to reconstruct the Late Pleistocene-Holocene floristic composition in an area of the northern Brazilian Amazonia, comparing the results with other Amazonian localities in order to discuss the factors that have influenced phytosociological changes over this time period. The work in eastern Marajó Island at the mouth of the Amazonas River was approached based on analysis of 98 pollen and diatom samples from core data distributed along a proximal to distal transect of a paleoestuarine system. The results indicated high concentration of *Rhizophora*, associated with arboreal pollen grains typical of the modern Amazonian rainforest during the last 40,000 cal yrs BP. Pollen composition also included wetland herbs. Diatoms were dominated by marine and fresh water taxa. Wetland forest, mangrove and, subordinately herbs, remained constant during most of the latest Pleistocene-early/middle Holocene. At 5,000 cal yrs BP, there was a distinguished change from forest and mangrove to wet grassland savanna due to sea level fluctuation. As marine influence decreased, the estuary gave rise to fresh water lacustrine and swamp environments, with establishment of herbaceous *campos*. A main conclusion from this study is that solely the occurrence of herbaceous savanna can not be used as a definitive indicator of past dry climates in Amazonian areas.

Key words: vegetation pattern, climate, late Quaternary, paleoenvironment, Marajó Island, northeastern Amazonia.

INTRODUCTION

Interpreting late Quaternary climate fluctuations in Amazonia based on vegetation changes is not yet an issue of overall consensus. For instance, pollen data from deep-sea fan hemipelagic and continental shelf sediments through the last 50,000 years support that the Amazonian rainforest was not extensively replaced by savanna during glaciation (Heberle and Maslin 1999, Kastner and Goñi 2003). In addition, several palynological studies suggest undisturbed closed forest during late Quaternary cooler climate episodes (e.g., Colinvaux et al.
1996, Haberle 1997, Bush et al. 2004, Irion et al. 2006, Mayle and Power 2008, Toledo and Bush 2008). On the other hand, cold forest is recorded in the upper Peniglacial of Ecuador (Colinvaux and Liu 1987). Cold and wet climate at the end of the Pleistocene, followed by a very dry phase that extended up to the middle Holocene, are recorded in several lagoons of the Llanos Orientales in Colombia (Behling and Hooghiemstra 1998). Dry climate was recorded during the Late Pleistocene and Holocene in the Cauca Valley of Colombia (Berrio et al. 2002), but there are records of humid phases during the early Holocene of Lake Fuquene, in Colombia (Van Geel B and Van der Hammen 1973), as well as in the middle to late Holocene of Lake Valencia (Venezuela) (Leyden 1985) and Lake Ayauch (Ecuador) (Bush and Colinvaux 1988).

In Brazil, there are many palynological studies suggesting undisturbed closed forest during cooler climate episodes of the late Quaternary (e.g., Colinvaux et al. 1996, Haberle 1997, Bush et al. 2004, Irion et al. 2006, Mayle and Power 2008, Toledo and Bush 2008). In contrast, several other studies, especially carried out in the seasonal eastern Brazilian Amazonia, have related savanna expansion to cool/dry episodes during this time interval (Absy et al. 1991, Van der Hammen et al. 1992, Van der Hammen and Absy 1994, Pessenda et al. 1998). For instance, the long paleoclimatic record of Carajás indicated three episodes of savanna development, i.e., >51,000 14C yr BP, 40,000 yr BP, and 23,000-11,000 14C yr BP (Absy et al. 1991). Climate drier than the modern one was also documented in this site between 7,900 and 4,500 14C yr BP (Sifeddine et al. 1994), which was correlated with a dry episode in the Humaitá area, southern of the State of Amazonas (Pessenda et al. 1998, 2001, Freitas et al. 2001). The Katira record in the State of Rondonia suggests prevalence of forest before 49,000 14C yr BP, and its replacement by savanna between 41,000 and 18,000 14C yr BP (Van der Hammen and Absy 1994). Paleontological (Webb and Rancy 1996, Vivo and Carmignotto 2004) and geological (Bibus 1983, Sifeddine et al. 2001) data sustain extensive areas of climate drier than the present one during the Late Pleistocene. Studies undertaken in several coastal areas of the Brazilian Amazonia revealed changes in vegetation due to other forces, for instance, sea level fluctuation (e.g., Behling and Costa 2000, 2001, Cohen et al. 2005). Other authors relate these changes to the increase in the Amazonas River discharge (Guimarães et al. 2011, Smith et al. 2011, 2012). It has been also proposed that modern occurrences of savanna in this region might be related to changes in coast morphology, rather than to climate (Rossetti 2010).

Considering the large dimension and high complexity of Amazonian ecosystems, the available information is still inadequate to fully provide insights on the mechanisms that might have influenced the evolution of plant communities in the latest Quaternary. Floristic variation needs to be recorded more precisely, and this must be based on interdisciplinary studies including paleontological proxies, particularly integrating them with sedimentological and stratigraphic analyses. We address this issue here by applying a palaeoecological approach based on pollen and diatom data. The first allows reconstructing the floristic successions through time. The later is a good proxy to differentiate among marine, estuarine and fresh water (e.g., lacustrine) paleoenvironments, as they have great sensitivity to physical, chemical and biological parameters, such as sediment supply, light intensity, salinity, pH, depth, trophic state, temperature and alkalinity (Round et al. 1990, Bennion 1995, Sylvestre et al. 2001, Resende et al. 2005, Hassan et al. 2006). In this work, these proxies are integrated with faciologic and stratigraphic analyses in order to tie the reconstruction of a paleoestuarine setting with late Quaternary plant successions. Therefore, the paleoenvironmental scenario results from integration of pollen, diatom, 14C dating, combined with sedimentologic and
stratigraphic data. Although not previously applied to Amazonian areas, this is an approach of high relevance to the reconstruction of paleovegetation patterns and to the analysis of the factors controlling plant evolution.

**PHYSIOGRAPHY AND GEOLOGY**

Marajó Island is part of a fluvio-marine archipelago bounded by the Atlantic Ocean (north), Pará River (south), Tocantins River-Marajó Bay (east), and Amazonas River (west). Climate is tropical, with a mean annual temperature of 28°C and precipitation of 2,500 to 3,000 mm/year. The topography is low, with a mean altitude of 12.5 m for the entire island, and between 2 and 6 m for its eastern side, where the study area is located. Vegetation consists of lowland, alluvial and dense Ombrophyla forests to the west, which are in sharp contrast with pioneer vegetation and grassland/woodland savanna or campos to the east (Fig. 2) (Miranda and Carneiro 1994, Rossetti et al. 2010). Mangrove and restinga are also recorded locally to the east (Cohen and Lara 2003).

Geologically, eastern Marajó Island is located in a poorly-known setting of the Pará Platform, bounded by the Mexiana Sub-Basin (northwest), Limoeiro Sub-Basin (southwest and west), Cametá Sub-Basin (south), Pará-Maranhão Basin (northeast), and Bragançina Platform (east) (Fig. 1). These structures, formed during the Equatorial South Atlantic opening, constitute the Marajó Graben System. Its sedimentary fill includes siliciclastic deposits of the Breves-Jacarezinho (Aptian-Cenomanian), Anajás (early Cretaceous) and Limoeiro (late Cretaceous) formations. These units (Fig. 2), formed in depositional settings ranging from alluvial fan, fluvial to shallow marine, are overlain by the mixed carbonate/siliciclastic Marajó Formation (Paleocene-Eocene) and sandstones and mudstones of the Tucunaré/Pirarucu Formations (Quaternary). On the surface, eastern Marajó Island contains an elongated belt of Miocene estuarine deposits of the Barreiras Formation and late Quaternary fluvial, aeolian and estuarine deposits of the Post-Barreiras Sediments (Rossetti et al. 1989, Castro et al. 2010). Nearby Lake Arari, where the study area is located, the Post-Barreiras Sediments display a 10 km wide and 40 km long, funnel-shaped paleomorphology related to a paleoestuary distant 45 km from the modern coastline.

![Location map and geology of the study area in eastern Marajó Island, Amazonas mouth.](image-url)

Previous studies integrating geomorphological, sedimentological, stratigraphic, isotopic ($^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N) and $^{14}$C data from eastern Marajó Island recorded Late Pleistocene and Holocene (i.e., 42,580 $^{14}$C yr BP to 3,340 $^{14}$C cal yr BP) fine- to coarse-grained, parallel-laminated or cross stratified sands, massive or laminated muds and heterolithic deposits (Castro et al. 2010). According to these authors, these proxies indicate that the organic matter in the sediments derived mostly from marine and fresh water phytoplankton sources. These data, combined with facies associations, indicated fluvial channel, floodplain, tidal channel/tidal flat, central basin, tidal delta, and
tidal inlet/sand barrier environments, consistent with estuaries. Additionally, the following changes in relative sea-level were proposed: a main rise from 8,360-8,180 cal yr BP to 6,299-6,175 cal yr B.P (i.e., before the worldwide mid-Holocene transgressive peak); and an drop after this time length. The latter fall led to the progressive establishment of continental conditions as the coast prograded around 45 km northward, culminating with replacement of the estuarine system into the modern Lake Arari.

**MATERIALS AND METHODS**

This study was based on the analysis of 98 pollen and diatom samples (0.5 cm³) from a total of 66 m of cores derived from five shallow drills (i.e., TSM4, TSM8, TSM10, TSM11 and TSM12). These were distributed a proximal-distal transect along the studied estuarine paleomorphology (Fig. 3). The core data, collected in the context of a previous faciologic and stratigraphic study (Castro et al. 2010), were obtained with a percussion drilling Robotic Key System (RKS), model COBRA mk1 (COBRA Directional Drilling Ltd., Darlington, U.K.). Seventeen wood, charcoal and organic sediments were dated by accelerator mass spectrometer (AMS) at the Beta Analytic Radiocarbon Dating Laboratory. Possible contaminants, as modern roots, were eliminated manually during the pre-treatment. In the following, the organic matter from sediments was extracted according to the laboratory standard pre-treatment with acid wash. This procedure attempted to remove recent organic matter or ancient organic matter in slow decomposition process, adsorbed in the sediments, providing carbon younger than the average carbon in the samples. The serial rinses eliminated all contaminants as associated sediments and rootlets. Conventional ¹⁴C ages were calibrated to calendar years using the Pretoria Calibration Procedure program (Talma and Vogel 1993).

Pollen extraction followed standard techniques with HCl, KOH, HF, and acetolysis (Faegri and Iversen 1989). Pollen concentration in grains/cm³ was determined adding one tablet of *Lycopodium*...
Pollen and spore data are presented in the pollen diagrams as percentages of the total pollen sum. For percentage calculation, ferns and aquatic spore taxa were excluded from the total sum.

Preparation of diatom samples was based on 30% H$_2$O$_2$ and 10% HCl. The diatoms were mounted in slides using Naphrax. Identification was based on the author’s own reference collection, as well as several published diatom morphological descriptions (e.g., Round et al. 1990, De Oliveira and Steinitz-Kannan 1992, Metzeltin and Lange-Bertalot 1998, Houk 2003). A minimum and maximum of 200 and 500 valves, respectively, were counted for each slide. Identification, counting, as well as sum, percentage and concentration calculations followed the same procedure adopted for pollen analysis.

**PALEOECOLOGICAL DATA**

Among the analyzed drills (i.e., TSM4, TSM8, TSM10, TSM11, and TSM12) (Figs. 4 to 8), only samples from TSM8, located to the south of the paleoestuary, and eight samples (i.e., MR248 to MR258) from the base (i.e., between 11.0 and 16.0 m depth) of TSM4, located near the eastern margin of this system, contained pollen grains in quantities suitable for statistical analysis. Diatoms were abundant in TSM10 and TSM11, located in the distal and middle estuary, where pollen grains were not present. In addition, diatoms were also statistically well represented in the uppermost two samples (MR290 and MR291) of TSM8. Samples derived from the other drills (i.e., TSM4 and TSM12) did record diatoms, but not enough for quantitative analysis.

**Pollen description**

**TSM4**

Three pollen zones are present, between depth intervals 16.5-14.5 m, 14.5-13 m and 13-11.5 m, the latter recording non-calibrated ages of 41,582 (±1,430) $^{14}$C yr BP and 42,580 (±1,430) $^{14}$C yr BP (Fig. 4; Tab. I). These deposits were formed in fluvial channel, floodplain and tidal channels or tidal flat environments. Palynomorphs were absent in all 13 samples analyzed in the interval above 11.5 m, corresponding to deposits with ages between 8,360-8,180 cal yr BP and 5,740-5,600 cal yr BP related only to marine-influenced settings (i.e., tidal channel or tidal flat, tidal delta, and estuarine central basin).
Fig. 4 - Diagram of pollen taxa percentages from TSM4. The three palynological zones recognized by CONISS diagram are also included in this diagram, as well as the available $^{14}$C ages (see text for descriptions). (Numbers to the left are $^{14}$C calibrated ages unless specified as *=non-calibrated age; MR 231-MR258=analyzed samples; A=central basin; B=tidal delta; C=tidal channel; D=tidal flat; E=fluvial channel; F=floodplain).
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Zone I: 16.5-14.5 m

Pollen concentration varies between 11,101 and 11,875 grains/cm³. Arboreous types are relatively constant, with concentration between 5,743 and 6,608 grains/cm³. Taxa such as Alchornea and Euphorbiaceae are the most frequent, with percentages ranging from 13.9-16.7% and 9.5-11.3%, respectively. Other arboreous elements are Arecaceae (2.6-5%), Euterpe (0.9-5.4%), Malpighiaceae (5.4-7.4%), Mauritia (1-4%) and Moraceae/Urticaceae (3.3-6.5%). Mangrove pollen occurs in concentration between 496 and 1,158 grains/cm³, being mainly attributed to Rhizophora (4.2-10.4%). Among herbaceous taxa, Poaceae (7.8–9.2%) revealed to be the most abundant type, followed by Asteraceae (3.9–6.3%), Borreia (2.1–6.4%) and Cyperaceae (1.7–5.4%). Cyathea (30-40%) is the most common fern spore type with its occurrence increasing toward the top of this zone. Macrophytes, such as Ludwigia and Myriophyllum, were present in low frequency.

Zone II: 14.5-13 m

The concentration of pollen grains fluctuates between 5,890 and 1,158 grains/cm³. The most abundant taxa are dominated by the arboreous elements Alchornea (18.4–23.7%), Malpighiaceae (5.4–7.1%) and Moraceae/Urticaceae (1.6–6.4%). These pollen grains show no significant differences in percentages when compared to zone I (Fig. 4). Arboreous pollen grains with low percentages are Arecaceae, Euphorbiaceae, Euterpe and Mauritia. Rhizophora pollen (0.5–6.4%) remains as the most representative of mangrove, with subordinate occurrences of Melastomataceae/Combretaceae (0.5–3.4%) and Avicennia (0.5%). Herbaceous pollen varied between 22.7 and 33%, with higher percentage of Poaceae (6.9–20.2%) than the previous zone. Cyperaceae is the second most abundant herbaceous element (2.5–14.4%).

Zone III: 13-11.5 m

Pollen concentration varies between 7,513 and 9,764 grains/cm³. Arboreous grains are the most abundant (67.7–69.7%), including mainly Alchornea (23.1–23.7%), Euterpe (2–4.8%), Malpighiaceae (7.1–7.7%) and Moraceae/Urticaceae (4.5–11.1%). Mangrove pollen grains occur in lower percentage relative to the previous two zones. Avicennia is not recorded and Rhizophora grains range between 0.5 and 6.4%. Herbaceous grains range from 19.7-22.7%, consisting mainly of Poaceae (9.1–19.4%) and Cyperaceae (6.6–7.2%). Asteraceae (2.9–5.6%) decreases in relation to the other two zones and Borreia is <1.5%. The ferns spores Cyathea and Polypodium vary from 30-40%-6-10%, respectively.

TSM8

Four zones were delimited in this core, correspondent to the depth intervals 18-11.7 m; 11.7-8.4 m; 8.4-2.4 m and 2.4-0.9 m (Fig. 5). The base of zones I and IV reported ages of 41,080 (+810) ¹⁴C yr BP and 7,250-6,900 ¹⁴C cal yr BP, respectively (Tab. I).

Zone I (18-11.7 m)

Concentration was significantly higher than in the previous drill, i.e., 22,389-56,886 grains/cm³. Mangrove pollen grains were the most abundant, i.e., 12,164-35,080 grains/cm³ being Rhizophora (51.7-70%) the most abundant taxon. The percentage of arboreous components varied from 21.3-36.1%, with Alchornea (15–25.8%), Euphorbiaceae (16.8–27%) and Moraceae/Urticaceae (1–6.7%) being the most frequent types. Herbaceous pollen varies

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Fig. 5 - Diagram of pollen taxa percentages from TSM8. The three palynological zones recognized by the CONISS are also included, as well as the available $^{14}$C ages (see text for descriptions).
from 4.3-12.3%, with Poaceae (4.3–8%) being the most abundant. The percentage and concentration of arboreal pollen increase uniformly upward in this zone. Mangrove pollen, particularly Rhizophora (Fig. 5A-B), have maximum concentration and frequency at the base and top of this zone. There is a direct correlation between concentration of arboreal and mangrove taxa, with herbaceous grains displaying constant concentration and percentage values along this zone.

**Zone II (11.7 to 8.4 m)**

Represented only by the sample MR301 (Fig. 5). Concentration corresponds to 44,599 grains/cm³. Arboreal grains are the most abundant including mostly Alchornea (23.3%) and Myrtaceae (6.7%). Mangrove representatives include low percentage of Melastomataceae/Combretaceae (17%) and Rhizophora (0.3%) pollen. Among herbaceous grains, Poaceae (9.7%) remains the most frequent type.

**Zone III (8.4 to 2.4 m)**

Analysis of samples MR293, MR294, MR297 and MR299 shows a total absence of palynomorphs.

**Zone IV (2.4 – 0.9 m)**

Pollen concentration is even higher than zones I and II, ranging from 46,229 to 77,429 grains/cm³. This zone has a remarkable change in composition (Fig. 5), indicated by dominance of mangrove pollen (69.8%) mainly consisting of Rhizophora (sample MR291) and high percentage of herbaceous pollen (66.7%), mostly represented by Poaceae (sample MR290). Mangrove grains in the latter include a low percentage of Rhizophora (0.7%). Arboreal elements occur throughout this zone, varying from 22.6-31%, with Alchornea (8.6-20%), Moraceae/Urticaceae (6.0–9.6%) and Fabaceae (0.3–4.3%) being among the most abundant taxa.

**Diatom description**

Analysis of the 390 diatom slides led to the identification of 41 taxa, of which 26 are typical of marine and 15 of continental environments.

**TSM8**

A total of 16 samples were analyzed in this drill, but diatoms were only recorded in the uppermost samples MR291 and MR290 (Fig. 6). This overall low volume in diatoms precluded to run statistic analysis. However, the two samples documenting diatoms displayed six marine species, and five species and three continental genera. The uppermost sample MR290 contained mainly continental diatoms consisting of benthic epiphytic species Eunotia zygodon (63%). The only marine species is Nitzschia granulate, which occurred in low percentage (i.e., 0.4%). Sample MR291 displayed exclusively marine diatoms, with Diploneis gruendleri (40.6%), Paralia sulcata (34.2%) and Nitzschia granulata (14.6%) being the most abundant taxa. These diatoms occurred in lacustrine deposits dated as 7,250 and 6,900 cal yr BP.

**TSM10**

The diatom zones contain chiefly marine taxa, except for the samples located between the depth intervals 1-0 m and 24-19 m (Fig. 7). Five zones are present. Zone I includes samples from the depth interval 24-16.8 m, which recorded the ages of 29,340 (±200) 14C yr BP, 7,420-7,170 cal yr BP and 6,950-6,740 cal yr BP and zones II to V are in the depth intervals 16.8-11.9 m, 11.9-8.4 m, 8.4-3 m and 3-1 m, respectively (Tab. I).

**Zone I (24-16.8 m)**

The most frequent taxa are Actinoptychus splendens (19.9-53.0%), Paralia sulcata (6.1-
Fig. 6 - Diagram of diatom taxa percentages from TSM8. The three palynological zones recognized by CONISS are also included in this diagram, as well as the available $^{14}$C ages (see text for descriptions).
Fig. 7 - Diagram of diatom taxa percentages from TSM10. The three palynological zones recognized by CONISS are also included in this diagram, as well as the available 14C ages (see text for descriptions).
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44%), Coscinodiscus radiatus (1–27.8%) and Coscinodiscus sp1 (6.5–12.1%). Actinoptychus splendens is relatively constant in the two lowermost samples, with significant upward decrease. Coscinodiscus radiatus also decreases upward, whereas the continental species Aulacoseira granulata occurs in low frequency (1.2%) throughout this zone.

Zone II (16.8–11.9 m)

This zone consists mostly of the marine taxa Actinoptychus splendens (18.5–55.4%), Coscinodiscus radiatus (17.9–44.9%), Paralia sulcata (1.7–20.4%) and Triceratium favus (1.5–4.4%). Aulacoseira granulata (0.7–4.1%) is more frequent in this zone that in the previous one. The percentage of Coscinodiscus sp1 and Thalassiosira sp4 increases upward, mostly at 13.8 m depth.

Zone III (11.9–8.4 m)

Actinoptychus splendens (22.8–62.4%) and Paralia sulcata (9.3–22.4%) are the most frequent taxa in this zone. Coscinodiscus radiatus is absent and Aulacoseira granulata does not exceed 3.2% in one sample at the base of this zone. Likewise in the previous zone, the percentage of these taxa varies along this zone. Actinoptychus senarius shows higher abundance (1.2–10.7%) in the lowermost sample, with a strong decrease in the two uppermost samples. Triceratium favus (1.1–3.4%) is less abundant than in zone I. The most frequent genera include Coscinodiscus sp1 (11.2–34.7%), Coscinodiscus sp4 (1.2–11%) and Thalassiosira sp1 (1.8–7.6%).

Zone IV (8.4–3 m)

This zone also displays only marine diatoms, with the highest values of Actinoptychus splendens (28–70.2%), Coscinodiscus radiatus (0.6–19.6%) and Paralia sulcata (1.9–22.4%). The continental Aulacoseira granulata does not exceed 3%, similar to zone III. Triceratium favus and Actinoptychus senarius occur in low percentages, i.e., 1–2.3% and (0.6–3.4%), respectively, though the latter is also well represented along this zone.

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Fig. 8 - Diagram of diatom taxa percentages from TSM11. The three palynological zones recognized by CONISS are also included in this diagram, as well as the available $^{14}$C ages (see text for descriptions).
Cymathoteca sp1, Diploneis gruendlerii and Nitzschia granulata are more abundant in this zone that in zones I, II and III.

Zone V (3-1 m)

There is only one sample represented in this interval, which lacks diatoms.

TSM11

The diatoms in this drill are almost exclusively marine. Five zones were recognized between the depth intervals 18-16 m, 16-13.4 m, 13.4-10.2 m, 10.2-7 m and 7-5.3 m. The base of zone 1 and the top of zone 5 recorded ages of 10,270-10,172 cal yr BP and 3,440-3,240 cal yr BP, respectively (Fig. 8).

Zone I (18-16 m)

The most frequent marine taxa are Actinoptychus splendens (33.0%) and Coscinodiscus radiatus (37.5%). Taxa with low percentages are Paralia sulcata (13.8%) and the continental species Aulacoseira granulata (7.9%). The species Triceratium favus does not exceed 1.6%.

Zone II (16-13.4 m)

Actinoptychus splendens (30–40.5%), Coscinodiscus radiatus (8.2–43.3%) and Paralia sulcata (13.6–19.4%) are the most common types. Coscinodiscus radiatus occurs in low percentage in the lowermost sample, but it increases slightly in the intermediate sample, to decrease again in the topmost sample. Paralia sulcata increases upward. Aulacoseira granulata (5.2–8.3%) occurs in low percentage, though this species is relatively constant in all samples of this zone.

Zone III (13.4-10.2 m)

Actinoptychus splendens (47–58.6%), Coscinodiscus radiatus (2.2–28.2%) and Paralia sulcata (6.3–13.2%) are also the most frequent species. All taxa vary along this zone, mainly Coscinodiscus radiatus, which shows sharp decline in percentage values in the three topmost samples. Likewise zones I and II, Aulacoseira granulata (1–3.7%) occurs in low percentage, but its percentage also decreases significantly in the two topmost samples. Actinoptychus senarius was recorded for the first time in all samples of this zone. Coscinodiscus sp1 (16.5–22.9%) increases upward. The other genus, such as Coscinodiscus sp2 to sp9, as well as Thalassiosira sp1, sp2, sp3 sp4, sp5, present low frequencies throughout this zone.

Zone IV (10.2-7 m)

This zone is characterized by high values of Actinoptychus splendens (41.4–63%), Coscinodiscus radiatus (9.6–23.9%) and Paralia sulcata (10.3–13.4%). Coscinodiscus radiatus and Paralia sulcata increase upward. Actinoptychus splendens shows a slight oscillation, with increased percentage in the intermediate sample. Actinoptychus senarius occurs only in sample MR375.

Zone V (7-5.3 m)

This zone is characterized by a total absence of diatoms.

DISCUSSION

Pollen distribution is controlled by the type of depositional environment, with higher concentration in continental deposits. In the study area, these elements are well preserved, reflecting the floristic composition associated with the Arari paleoestuarine system, as well as surrounding drainage basin. Exceptions are a few Andean pollen types, such as Alnus and Hedyosmum, which evidence long distance pollen contributions.

Evolution of plant communities through time

Pollen taxa mostly including Alchornea, Arecaceae, Euphorbiaceae, Malpighiaceae and
Moraceae/Urticaceae, dominant in the study area, constitute common representatives of the Amazonian rainforest. The common occurrence of the families Moraceae/Urticaceae (i.e., Cecropia) is consistent with successions of pioneer vegetation (Colinvaux et al. 1999). Although with low frequency, the continuous record of Mauritia and Euterpe pollen grains in the drill TSM4 and their local occurrence in the drill TSM8 indicate continental areas with flooding episodes. Good preservation of the entire sculptural elements (i.e., spine) in the Mauritia indicates insignificant transport or reworking. This palm taxon suggests fresh water environments and is considered as an important wetland and marsh indicator (Colinvaux et al. 1999, Bush et al. 2004). Mauritia and Euterpe, among other Arecaceae, are currently well known from many Amazonian flooded areas (Almeida et al. 2004). Although in volumes statistically less significant, the herbaceous Ludwigia, Myriophyllum and the arboreal Macrolobium genera present in all three zones of the drill TSM4 are further evidence of wetland environments. The high frequency of Rhizophora pollen in the drills TSM4 and TSM8 (except in the uppermost sample) attests to the constancy of mangrove at or adjacent to depositional sites. Frequent association of Rhizophora and Melastomataceae/Combretaceae (mostly Laguncularia) pollen further supports the proximity with mangroves. Association of these pollen grains with Avicennia (i.e., zone 2 of TSM4) conforms to mangrove deposits, as the latter is an entomophilous taxon with low production, and thus low dispersion, in the environment (Cohen et al. 2005). Mangrove constitutes a depositional environment commonly associated with estuarine systems, which is in accordance with the paleoenvironmental model proposed for the study area with basis on the integration of remote sensing, sedimentological, isotope ($\delta^{15}N$ e $\delta^{13}C$), and C/N data (Castro et al. 2010).

The pollen assemblage also contained herbaceous elements during all depositional time. The volume of these pollen grains is generally low and remains constant relative to the forest pollen grains along all the three zones, indicating fairly stable temporal distribution of the plant community. Poaceae, the main representative of the herbaceous assemblage, usually did not exceed 20%. This concentration is lower than recorded in savanna areas, where this taxon usually ranges from 50 to 70% (Salgado–Labouriau 1997). Elements of Poaceae are often found mixed with forest in many Amazonian varzea and river bank environments (Colinvaux et al. 1999). The occurrence of Cyperaceae, together with Poaceae, Mauritia, Euterpe, fern spores, as well as other aquatic taxa (i.e., Macrolobium, Ludwigia and Myriophyllum) in the drill TSM4, indicates a plant community adjacent to wetland forests. $\delta^{13}C$ data derived from the intervals with increased percentage of herbaceous pollen revealed only C$_3$ plants (Castro et al. 2010), thus we interpret that the studied deposits are dominated by C$_3$ herbs. Around 90% of the herbs present in the modern landscape of eastern Marajó Island display $\delta^{13}C$ signal within range of C$_3$ plants (C.M. Lima, unpublished data). The presence of C$_3$ herbs, combined with arboreal elements and high frequency of fern spores, leads to suggest that the study area was dominated by Late Pleistocene-Holocene phytophysiognomy similar to the modern one.

Although the aforementioned discussion supports the coexistence of herbs with flooded forests and mangroves during most of the depositional time, an abrupt change from this vegetation pattern is suggested by the uppermost sample (i.e., MR290) of TSM8. In this sample, the tree components Alchornea, Fabaceae and Moraceae/Urticaceae, added to the anomalously high percentage of Poaceae (i.e., 66.7%), indicate wetland forest replacement by open areas with pioneer taxa, typical of first phase ecological successions, around 5,000 yrs BP. The subtle
disappearance of *Rhizophora* attests to mangrove retreat, reinforcing a drastic change in floristic composition during this time.

The absence of pollen and spore grains in most of the drills TSM10 and TSM11, as well as in the uppermost 11.5 m of the drill TSM4 and between 8.4 to 2.4 m of the drill TSM8, is attributed to an increased influence of marine phytoplankton. Increased washing by tidal currents and perhaps also oxidizing conditions must have precluded palynomorph preservation in these depositional intervals.

The prevalence of marine diatoms (*Actinoptychus splendens, Coscinodiscus radiatus, Paralia sulcata, Nitzschia granulata*) and their association with continental components (*Actinella sp1, Aulacoseira, Eunotia zygodon, Desmogonium e Pinnularia*) are consistent with organic matter mixing. This is in agreement with a depositional setting influenced by both marine and fresh waters, as typical of estuarine systems. In particular, *Eunotia* and *Actinella* are genera commonly reported in Amazonian acidic waters (Patrick 1940, De Oliveira and Steinitz-Kannan 1992, Ferrari et al. 2007). The frequent occurrence of the genera *Coscinodiscus* sp and *Thalassiosira* sp (i.e., TSM10 and TSM11) records brackish water conditions (Round et al. 1990). On the other hand, the dominance of fresh water diatoms and the overall lack of mangrove pollen grains in the uppermost sample of the drill TSM8 are related to the prevalence of relatively more continental conditions in the late Holocene.

**Comparison with other Amazonian records and influencing mechanism**

The pollen composition remained constant throughout most of the studied sections, regardless of climate fluctuations and transgressive-regressive episodes associated with the dynamic evolution of the coastline. In the latest Pleistocene and early/middle Holocene, the phytophisiognomy was one dominated by forest with wetland representatives in close proximity to mangrove and a low contribution of herbaceous components. However, a drastic vegetation change happened after 7,250-6,900 cal yr BP, i.e., in an estimated age of circa 5,000 cal yr BP (considering a constant sedimentation rate). These data must be analyzed together with the latest Pleistocene-Holocene record from other Amazonian areas.

Latest Pleistocene glacial dry climate episodes have been frequently interpreted in several Amazonian areas (e.g., Van Geel B and Van der Hammen 1973, Absy et al. 1991, Sifeddine et al. 1994, Van der Hammen and Absy 1994, Colinvaux et al. 1996, 1999, Behling et al. 2001, Berrio et al. 2002). Savanna expansion between 9,000 and 4,000 cal yrs BP has been also used to indicate an early to middle Holocene dry climate in this region (Absy et al. 1991, Mayle et al. 2000). Change from forest to savanna in southwestern Amazonia between 7,000 and 4,000 cal yrs BP has been related to dry periods (Pessenda et al. 2001). Drier climate would have also promoted lowering of lake levels in northeastern Amazonia between ca. 6,400 and 4,700 cal yrs BP (Toledo and Bush 2007). Lake Santa Ninha recorded the replacement of flooded forest by grasslands between 5,000 and 4,000 cal yrs BP (Moreira et al. 2009). On the other hand, no evidence of a strong mid-Holocene dry event was found in lakes near Prainha, central Amazonia (Bush et al. 2000). Furthermore, there is no indication of savanna development in the Caxiuanã pollen record, where there is a continuous record of forests for the last 7,870 (± 70) cal yrs BP (Behling and Costa 2001). Lake Calado, near Manaus, displayed dense tropical forest since 8,330 (± 50) cal yrs BP (Behling et al. 2001). However, localities of northeastern Amazonia record decline in the tropical forest during the mid to late Holocene, for instance at 7,640 and 6,620 cal yrs BP and after 3,630 cal yrs BP Lake Crispim (Behling and Costa 2001), as well as between 7,250 and 5,600 cal yrs PB and after 3,100 cal yrs BP in Lake Curuçá (Behling 2001).

The pollen data presented herein were not sensitive to record any forest fragmentation as a consequence of latest Pleistocene glacial dry climatic
episodes. Similarly, the subtle change in vegetation pattern detected around 5,000 cal yrs BP could not be related to drier past climatic episodes. This is because the herbaceous taxa, mostly represented by Poaceae, were adapted to wet environments, similar to herb representatives from modern wetlands of eastern Marajó Island. A vegetation change coeval with the one recorded in the study area occurs in other Amazonian areas. Hence, a marked change from dense tropical forest and mangrove to open flooded savanna was detected in Lake Marcio, State of Amapá, at c. 5,000 cal yrs BP (Toledo and Bush 2008). According to these authors, this event was attributed to lake isolation due to river floods, combined with increased paleofires mainly due to human occupation. In the Tapajós area, an overall continuous forest record was interrupted by a short episode of Poaceae increase between 5,500 and 4,200 cal yrs BP, which was also related to human activity superposed upon a long term change in hydrology during the late Holocene fall in sea level (Irion et al. 2006). Other studies undertaken in the Marajó Island show a relationship between marine influence and expansion of mangrove areas during the mid Holocene, followed by their replacement by forest and herbaceous vegetation in the late Holocene due to greater freshwater influence as the Amazonas River discharge likely increased (Smith et al. 2011, 2012). However, the dynamics of changes in the Amazonas River discharge through the Holocene remains to be confirmed in order to support this hypothesis. On the other hand, in the Amapá littoral, a similar mangrove dynamics has been recorded (Guimarães et al. 2011), but these authors noted that the increase in fluvial inflow did not result in replacement of mangrove by freshwater vegetation. In addition, there was a replacement of mangrove by swamp savanna in an area of Guyana at circa 5,000 cal yrs BP, possibly as a consequence of a sea level drop (Tissot et al. 1988).

For the particular instance of the study area, forest fragmentation due to human influence at nearly 5,000 cal yrs BP is highly unlikely, as archaeological vestiges in Marajó Island are younger, being recorded only after circa 2,000 yrs BP (Roosevelt 1991). It is also unlikely that the occurrence of savanna in this area is related to a past drier climate, because this change took place simultaneously to an overall increase in humidity that culminated with the rainforest expansion in the region (Baker et al. 2001, Sifeddine et al. 2001). A plausible hypothesis defended herein is that the remarkable change from forest and mangroves into the wet savanna, which still dominates the present landscape of eastern Marajó, might have been influenced by the geological evolution and relative sea level fluctuations recently proposed for this area (Castro et al., 2010). According to these authors, following the last significant rise in relative sea level between 8,360-8,180 cal yrs BP to 6,299-6,175 cal yrs BP, i.e. during the melting of the Younger Dryas Ice Sheet, eastern Marajó was undergone to sediment progradation due to seaward shoreline shift promoted by a drop in relative sea level. Tectonic reactivations might have contributed to enhance the signal of relative sea level changes in this area (Rossetti et al. 2007, 2012). As a result, the marine influence decreased and the estuarine depositional system and associated channels were naturally replaced by fresh water lacustrine and swamp environments. Considering these propositions, it is likely that this process might have been also the cause for the replacement of mangrove vegetation recorded in the proximity of the Lake Arari up to 4,000 yrs BP by wet grassland savanna (D.F. Castro, unpublished data, M.C.C. Miranda, unpublished data). Mangroves are very sensitive to environmental changes. We argue that the significant change in coastal morphology due to progradation triggered by tectonics in eastern Marajó Island might have promoted a disequilibrium in the optimum conditions needed to hold mangrove development in this area. Despite this interpretation, the hypothesis of increased river discharge suggested by other authors must be further tested as a potential element to have further contributed to the recorded change in vegetation types in this region.
Considering continuous deposition, the drop in relative sea level and the consequent environmental change recorded in eastern Marajó seems to have occurred rapidly. This is indicated by the close proximity (<40 cm apart) of the samples MR291 and MR290; the first dominated by marine diatoms and mangrove pollen grains, and the second with prevalence of Poaceae and forest pollen in association with fresh water diatoms. Despite this rapid change, fully continental environments with the establishment of fresh water lacustrine and swamp environments completed only recently, i.e., after circa 500 cal yrs BP, when Rhizophora pollen grains were vanished from the sedimentary record of this area (Cohen et al. 2008).

CONCLUSIONS

The pollen and diatom records from eastern Marajó Island are compatible with estuarine deposition, development of mangrove and mixed influence of marine, fresh and brackish waters. These records were not sensitive to detect any noticeable change in vegetation during the Late Pleistocene and early/middle Holocene, when the landscape was dominated by mosaics of wetland forest and mangrove. A drastic change occurred in the middle to late Holocene, with a remarkable increase in herb frequency, mostly Poaceae. This is related to amplification of swamp savanna, with a consequent progressive retreatment of wetland forest and mangrove. Such a change could not be related to human disturbance, as human occupation in the study area is record only after circa 2,000 cal yrs ago. The influence of a drier climate is also improbable, as Amazonia was undergone to increased humidity during the middle to late Holocene, which culminated with amplification of the tropical rainforest as we see today. The prevalence of C₃ herbs led to conclude that the origin of the herbaceous campos in this area dates back to the middle to late Holocene. It also suggests that, as in the present time, this vegetation pattern must have been originated under humid conditions.

Eastern Marajó was undergone to coastal progradation due to a fall in relative sea level in the middle to late Holocene. Paleoenvironmental changes resulting from this process must have been the main cause of vegetation change recorded during this time interval. As the estuary became abandoned, lakes and swamps developed, promoting the establishment of the herbaceous campos that are typical of eastern Marajó today. Therefore, the present study leads to state that the record of savanna in late Quaternary deposits of Amazonian areas should not be directly used to support past dry climates. The dynamics associated with the evolution of the depositional environments might have also played a crucial role. Therefore, previous interpretations of dry climates in Amazonia based on this type of proxy should be revisited.

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RESUMO

O objetivo deste estudo foi de reconstruir a composição florística do Pleistoceno Tardio-Holoceno em uma área da Amazônia Oriental, comparando os resultados com outras localidades amazônicas, a fim de discutir os fatores que influenciaram as mudanças fitofisionômicas. O trabalho no leste da Ilha Marajó, na desembocadura do rio Amazonas, baseou-se na análise de 98 amostras de pólen e diatomáceas derivadas de dados de testemunhos de sondagem distribuídos ao longo de um transecto proximal-distal de um sistema paleoestrurino. Os resultados indicaram alta concentração de Rhizophora, associada a grãos de pólen típicos da floresta Amazônica moderna durante os últimos 40.000 yrs BP. A composição palinológica também incluiu ervas de áreas alagadas. Diatomáceas são dominadas por táxons
marinhos e de água doce. Floresta inundada, mangue e, subordinadamente erva, permaneceram constantes durante grande parte do Pleistoceno Tardio-Holoceno inferior/médio. A 5.000 cal BP, houve mudança marcada de floresta e mangue para savana de gramíneas de áreas alagadas devido a flutuações do nível do mar. Com diminuição da influência marinha, o estuário foi substituído por ambientes de lago de água doce e pântanos, com estabelecimento de campos herbáceos.

Uma conclusão principal deste estudo é que a ocorrência de savana herbácea não pode ser usada como indicador para sugerir climas secos passados em áreas amazônicas.

**Palavras-chaves:** padrões vegetacionais, clima, Quaternário tardio, paleoambiente, Ilha do Marajó, Amazônia Oriental.

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