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Compositional and diversity comparisons between the palynological records of the Neogene (Solimões Formation) and Holocene sediments of Western Amazonia

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ABSTRACT

Western Amazonia underwent dramatic changes in its landscape and environments during the Neogene, which led to its extant, hyperdiverse, tropical rainforest. Although the palynological fossil record has been the most useful proxy for understanding the history of the Amazonian biome, the floristic composition and diversity of the Neogene and the present Amazonian environments have never been thoroughly compared. In this work, we present preliminary comparisons of the pollen content of a Miocene core from the Solimões Formation in western Amazonia (Brazil) with the pollen content of Holocene sediments from flooded environments (várzeas and lake margins) near the Miocene site. We found a total of 463 pollen and spore types (Miocene, $n = 284$; Holocene, $n = 231$), only 52 of which were shared. The Holocene flooding environments displayed distinct palynological signals; both the Holocene and Miocene palynofloras have pollen primarily sourced from the local, flooded environments, with no significant differences in within-sample pollen diversity. The Holocene palynoflora was more heterogeneous in composition than the Miocene palynoflora, probably because the Miocene wetlands (the Pebas System) were highly homogeneous at a continental scale, far more than modern western Amazonia, thus implying that the spatial vegetation turnover was much lower than in modern ecosystems.

KEYWORDS
Amazonia; palynology; Miocene; Holocene; Solimões Formation; floristic diversity

1. Introduction

The Amazonian forest is the most diverse in the world (Thomas 1999), and yet the origin of its great diversity is poorly understood. Hypotheses include: low rates of extinction and/or high rates of origination; migration events from Africa and North America that could have contributed up to 20% of extant Amazonian biodiversity (Pennington and Dick 2004); and rapid evolutionary turnover (Antonelli et al. 2015). The paleobotanical record indicates that during the Paleocene the floristic composition of northern South America was very similar, at the family level, to the current composition of Neotropical rainforests (Wing et al. 2009) and that those families have continued to dominate lowland Neotropical forests until modern times (Ricklefs and Renner 2012), with the Amazon biome being the main source of Neotropical biodiversity (Antonelli et al. 2018). A key to fully understanding why Amazonia has such high biodiversity is its plant fossil record, which allows us to assess extinctions over evolutionary time, and thus measure rates of diversification (origination versus extinction).

The modern landscape of Amazonia, including the Amazon River, was established by the late Miocene to Pliocene (Hoorn et al. 2010). During the early and middle Miocene, most river drainages of western Amazonia ran westward and northward, opposite to the current eastward direction (Caputo and Soares 2016; Figueiredo et al. 2009). Due to high rates of subsidence driven by processes related to the Andes uplift and dynamic topography (Shephard et al. 2010), most of western Amazonia was occupied by an ecosystem without a modern analogue, the Pebas System (Wesselingh et al. 2002), which existed from ∼23 to ∼10 Ma (Hoorn 1993; Wesselingh 2006; Hoorn et al. 2010; Jaramillo et al. 2017). This continental-scale system was composed mostly of a mixture of deltaic plains, low-energy wetlands with swamps, ponds, and channels, extensive floodplains and shallow freshwater lakes (Wesselingh et al. 2002; Jaramillo et al. 2017). Most of the drainage of western Amazonia ultimately was discharged into the Caribbean Sea via the Orinoco/Llanos region in Colombia and Venezuela (Jaramillo et al. 2017). Two short-lived marine episodes occurred during the Pebas interval, the first during the early Miocene and the second during the middle Miocene (Boonstra et al. 2015; Jaramillo et al. 2017). This marine influence probably had effects on the floristic composition of the Amazon forest as plant groups adapted to the newly formed environments (Bernal et al. 2019). The Pebas System ended during the late

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Miocene (~9.4 Ma) with the onset of the modern Amazonian fluvial drainage flowing eastward (Wesselingh et al. 2002; Hoorn et al. 2017).

Palynological data have been used to assess the floristic composition and diversity changes of Amazonia throughout geological time (Van der Hammen 1954; Germeraad et al. 1968; Regali et al. 1974; Lorente 1986; Muller et al. 1987; Hoorn 1993, 1994a, 1994b, 2006; Behling et al. 2010; Hoorn et al. 2010; Jaramillo et al. 2010a, 2017; Silva-Caminha et al. 2010; Boonstra et al. 2015; Silveira and Souza 2015; Kachinasz and Silva-Caminha 2016; Salamanca et al. 2016; Silveira and Souza 2016, 2017; Leite et al. 2017; Linhares et al. 2017; D'Apolito et al. 2019; Hoorn et al. 2019). However, comparing the diversity and composition of extant Amazonian floras with the fossil palynological record is not a straightforward process. Many taphonomic factors affecting the pollen record need to be taken into account first. A useful approach is to compare the fossil record with the Holocene record, because the Holocene pollen record probably has been through the same taphonomic filters as older pollen. Initial attempts using this approach include those of Hooghiemstra and Van der Hammen (1998) and Van der Hammen and Hooghiemstra (2000), who compared the number of pollen types found in Miocene sediments in northern South America (Hoorn 1994a) with the number of pollen types found in recent sediments (Urrego 1994) and found more ($n = 280$) in the Miocene palynoflora than in the recent palynoflora ($n = 140$). Jaramillo et al. (2006) compared the species richness of a Holocene palynoflora from Colombia derived from the literature with that of a palynoflora from Paleogene to lower Miocene strata from northern Amazonia and the Llanos of Colombia, and found the Holocene palynoflora to be more diverse. However, when comparing the palynofloral diversity of Miocene and Holocene samples from Amazonia, Jaramillo et al. (2010a) observed no significant difference in diversity, although the sample size was small.

Any comparison between Holocene and pre-Holocene palynofloras using data derived from the literature alone is problematic because of methodology. Often, palynologists studying Holocene sediments and paleopalynologists are dealing with different sets of research questions, and therefore the ways they count pollen may not be comparable. Quaternary palynologists group pollen types according to botanical affinities (e.g. Arecaceae, Melastomataceae, Myrtaceae, etc.) and often do not distinguish morphotypes within major groups (e.g. several distinct morphotypes within Arecaceae would be lumped into a single group), whereas paleopalynologists group them according to morphology (e.g. *Psilamonocolpites* type 1, *Psilamonocolpites* type 2, etc.). Many Quaternary palynologists do not count spores or morphotype them, whereas spores are often important biostratigraphical markers in pre-Quaternary palynology. These counting differences can create artificial differences in abundance distribution and diversity.

Here, we use the same counting method to compare a set of Miocene and Holocene samples from western Amazonia. We aim to answer the following questions: (1) which palynoflora is more diverse?; (2) how similar are the two palynofloras in composition?; (3) are modern floodplains more or less heterogeneous in pollen composition than Miocene samples?; and (4) what environmental groups compose the pollen counts of the two palynofloras? Considering the importance of the Miocene in the establishment of today's Amazonian environment and the gaps in our knowledge of how its high biodiversity was produced, these comparisons will provide a baseline for understanding when and how Amazonia reached its modern levels of biodiversity.

2. Study area

2.1. Solimões Basin and Formation

The Solimões Basin is a large intracratonic sedimentary basin (500,000 km^2) that extends over northwestern Brazil, Ecuador, Perú, and Colombian Amazon (Figure 1A). It is bounded to the west by the Iquitos Arch, to the east by the Purus Arch, and to the north and south by the Proterozoic rocks of the Guiana Shield and central Brazil, respectively. The Solimões Formation is composed of sandstones, siltstones, and claystones with layers of shells and lignites and contains a rich fossil record (Maia et al. 1977; Eiras et al. 1994). Dated as Miocene (Cruz 1984; Hoorn 1994a; Silva-Caminha et al. 2010; Jaramillo et al. 2017; Leite et al. 2017), it forms a sedimentary wedge from the Purus Arch to the sub-Andean basins, reaching more than 2000 m in thickness toward the west (Maia et al. 1977; Maia and Marmos 2010) (Figure 1A).

2.2. Extant várzea vegetation

Várzeas are areas periodically flooded by sediment- and nutrient-rich white-water rivers (e.g. the Solimões River). These floodplains include lakes formed between bars, in abandoned river meanders, in depressions, and in old tributary valleys (Junk et al. 2012), all formed by fluvial processes (Latrubesse 2012). In the extant Amazon Basin, approximately 3% of the area is composed of várzea forests (Junk 1992, 1997). The várzea vegetation is less species rich than terra firme (Prance 1979) and trees display a variety of morphological and physiological adaptations to flooding (Parolin et al. 2002; Wittmann et al. 2006). In western Amazonia, 85–90% of the várzea forest is classified as low várzea (i.e. >3 m water level for >50 days/year; Wittmann et al. 2002). In contrast, high várzeas experience <3 m water level for <50 days/year, occupying transitional areas between flooded and non-flooded sites. Late successional forests in high várzeas are richer in tree species and more heterogeneous, whereas low várzeas in western Amazonia are more similar among themselves (Wittmann et al. 2006).

Floodplain forest censuses from western Amazonia, including Brazil, Colombia, Ecuador, Peru, and Bolivia (Wittmann et al. 2006), show that the most abundant plant families are Fabaceae, Euphorbiaceae, Malvaceae (Bombacoideae), Moraceae, and Arecaceae. Some of the most important plant species are the bombacoid tree *Pseudobombax munguba* and palm trees (Wittmann et al. 2006). In early stages of succession, *Alchornea* (Euphorbiaceae) forms monospecific stands along with

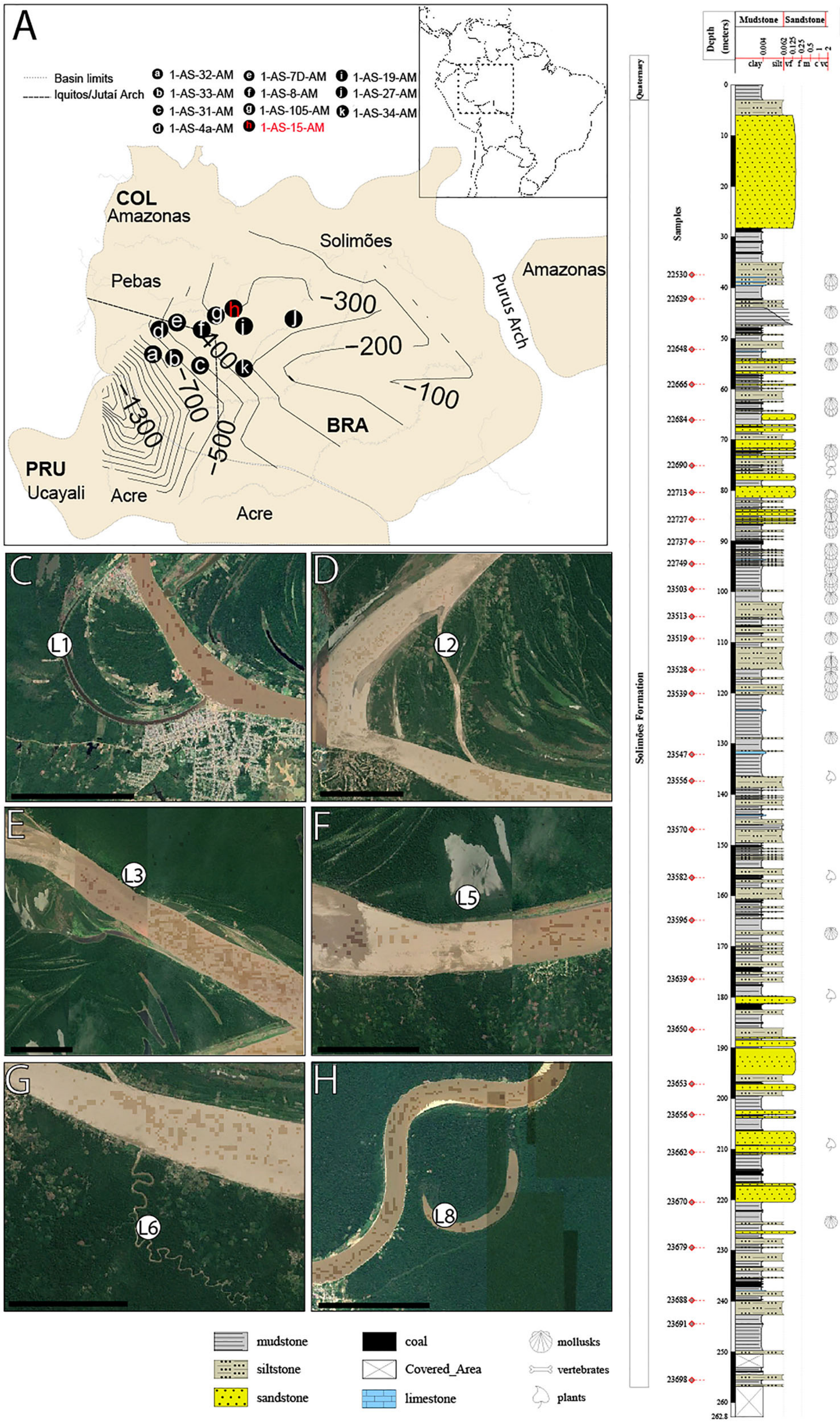

Figure 1. (A) Outline of the Solimões/Amazonas/Ucayali basins and isopach lines of the Solimões Formation (adapted from D'Apolito 2016); location of Brazilian Geological Survey (CPRM) cores studied by Latrubese et al. (2010) (a), Leite et al. (2017) (b), Kachinasz and Silva-Caminha (2016) (c, k), Hoorn (1993) (d), Linhares et al. (2017) (e), (f), Jaramillo et al. (2017) (g), this study (h), Silva-Caminha et al. (2010) (i, j). (B) Lithological description of core 1-AS-15-AM, 0 to 262.8 m, highlighting the analyzed pollen samples. Holocene sampling sites include (C) L1, (D) L2, (E) L3, (F) L5, (G) L6 and (H) L8. Source: Google Earth Pro 2019

grasses, *Cecropia*, and pteridophytes (Kalliola et al 1991; Wittmann et al. 2004), sometimes forming floating meadows (Absy 1979; Roucoux et al. 2013). Várzea lakes can be found with a dense macrophyte and herbaceous cover, but also there are floodplain indicator trees such as *Cecropia* and *P. munguba* (Junk et al. 2012).

3. Methods

3.1. 1AS-15-AM core

The 1AS-15-AM core (−4.01 S, −69.489 W) is ca. 250 m thick and is located near Tabatinga (Amazonas, Brazil) in the upper Solimões Basin (Figure 1A). It was drilled by the Brazilian Geological Survey (CPRM) in the 1970s. The borehole cored the Solimoes Formation which is composed mostly of mudstones, sandstones, and siltstones, with limestone and lignite present (Maia et al. 1977) (Figure 1B). Thirty samples were processed and analyzed for palynological content. Processing included disintegration of samples with a hammer and separation of 10 cm^3 of sediment; elimination of carbonates with concentrated hydrochloric acid for a minimum of 12 hours; and removal of silicates with concentrated hydrofluoric acid for a minimum of 24 hours (Wood et al. 1996). After these steps, the material was washed with distilled water to neutralize the acids and sieved in 250-μm and 10-μm meshes to eliminate coarse and very fine organic residues, respectively. The >10 μm fraction was then disintegrated in an ultrasonic bath and the portion of less dense organic matter was recovered. This residue was cleaned in an ultrasonic bath for a few seconds and concentrated in a centrifuge. Slides were mounted with Eukitt. All processing was performed by Paleoflora Ltd., Colombia.

3.2. Holocene

Seven shallow cores, each 60 cm deep, were collected across several active sedimentary environments near Tabatinga. Sites L1 (−4.36 S, −70.05 W), L2 (−4.35 S, −69.97 W), L3 (−4.33 S, −69.85 W), and L6 (−4.40 S, −69.96 W) were collected in várzea (floodplain), whereas L5 (−4.39 S, −69.87 W) and L8 (−4.35 S, −70.17 W) were collected from lake margins in the inner parts of the floodplains, thus still subject to periodic flooding although for shorter periods (Figure 1C). Dense tropical rainforest occupies the region (IBGE 1977). The Holocene shallow cores are all composed of muds deposited in recent, fine-grained settings. They are homogeneous and do not display significant changes in colour, texture, or structure. Three samples per profile were taken, every 10 cm, to reach a total of 21 samples. Samples were treated with potassium hydroxide 10% (Faegri and Iversen 1966) to remove humic acids, filtered through a 250-μm mesh to remove coarse residues, acetolyzed (Erdtman 1952), and gravitationally separated with heavy liquid using a mixture of bromoform and ethyl alcohol in a ratio of 2:1 (Kummel and Raup 1965). Slides were mounted with glycerine gelatin and sealed in paraffin. Processing was performed at the Laboratório de Palinologia of Instituto Nacional de Pesquisas da Amazônia (INPA).

3.3 Palynological analysis

Pollen slides were analyzed at Laboratório de Palinologia of INPA using a Primo Star (Zeiss) optical microscope at magnifications of 40× and 100×. A minimum of 300 spores and pollen grains were counted per sample. For taxonomic identification of fossil pollen types we consulted works on Neogene palynology of northern South America (Germeraad et al. 1968; Lorente 1986; Muller et al. 1987; Hoorn 1994a; Silva-Caminha et al. 2010; D'Apolito 2016) and the Morphological Electronic Database of Cretaceous–Tertiary and Extant Pollen and Spores from Northern South America (2014) which has up-to-date information on pollen and spores from the Cretaceous and Cenozoic for northern South America. To identify Holocene pollen types, we consulted the pollen reference collection of INPA and the works of Absy (1979), Roubik and Moreno (1991), Colinvaux et al. (1999) and Lorente et al. (2017). Holocene palynomorphs were named according to the taxonomy used for Miocene palynomorphs to allow comparisons.

All morphotypes were assigned a botanical affinity when possible. Taxa were divided into several ecological environments: flooded (F) if the taxon is restricted to flooded environments (e.g. várzea, lake margins); non-flooded (NF) if present only in non-flooded areas (e.g. terra firme); flooded/non-flooded (FNF) if present in both flooded areas and terra firme; aquatic; mangrove; and montane (Supplementary Table 1). Samples were classified into three main lithological categories (mudstone, siltstone, and sandstone).

A nonmetric multidimensional scaling (nMDS) analysis, using the Chao dissimilarity index (Chao et al. 2004), was performed to assess similarities between samples and taxa. The Chao index takes into account abundances and the number of unseen species pairs (Chao et al. 2004). Singletons were removed and the package Vegan v. 2.4-4 was used (Oksanen et al. 2017) to run the analysis. To assess the significance of difference of means between two groups we used a Student t-test, and we used an analysis of variance (ANOVA) when several groups were compared. Sample similarity was calculated using both the Chao dissimilarity index and the Euclidean distance of the nMDS analysis (distance between two points in a multidimensional space; Gordon 1999) using the package Vegan (Oksanen et al. 2017).

Sample richness was calculated with the sample coverage method (Chao and Jost 2012) using the iNEXT v. 2.0-15 package (Hsieh et al. 2018). The Shannon index (H'), a diversity measurement that takes into account the degree of evenness in species abundances (Magurran 2004), was calculated using the package Vegan (Oksanen et al. 2017). Species accumulation curves, that give the expected number of observed species as a function of sampling effort (Deng et al. 2015), were also calculated using Vegan (Oksanen et al. 2017). These were used to compare the sampling effort between Holocene and Miocene samples.

The 15-AM core was dated by performing graphic correlation (Edwards 1989) with core 105-AM (Jaramillo et al. 2017) of the Solimões Formation, which is 55 km to the west. Core 15-AM is isochronous with the upper ∼280 m of core 105-AM, which ranges from 17.8 to 10.7 Ma. We identified palynozone T16 from 37.5 m to 94.5 m (∼10.7 to 12.7 Ma), T15 from 94.5 m to 109.25 m (12.7 to 14.2 Ma), T14 from 109.25 m to 146.9 m (14.2 to 16.1 Ma) and T13 from 146.9 m

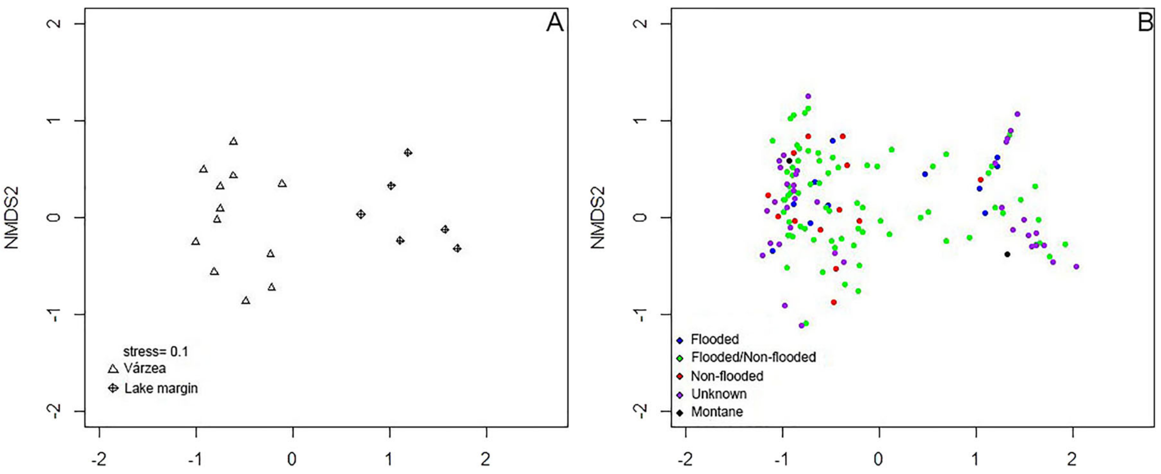

Figure 2. Non-metric multidimensional scaling of the Holocene samples. (A) Samples separated according to várzea and lake margin environments. (B) Species do not cluster according to ecological preference (flooded, non-flooded, flooded/non-flooded, unknown and montane).

to 255.5 m (16.1 to 17.8 Ma) (palynozones follow Jaramillo et al. 2011).

All analyses were done using R language v. 3.4-2 (R Development Core Team 2018). R scripts used to perform the analyses of this paper are given as Supplementary Material 1. Pollen counts are given in Supplementary Table 2.

4. Results

4.1. Holocene flooding environments

Comparing the pollen composition of our Holocene samples from the different flooding environments produced two distinct groups along axis 1 of the nMDS (t-test, df = 11.04, $p < 0.001$, nMDS stress = 0.13). The two groups correspond to várzea and lake margin environments (Figure 2A). Species do not cluster together according to the forest type they belong to (Figure 2B). Only 14% of taxa are shared between the two environments, representing 68.5% of total abundance. The five most abundant types in várzea are Poaceae, *Polypodium* sp. 1, *Polypodium* sp. 2, *Polypodium* sp. 3, and *Microgramma*, whereas the five most abundant types in lake margin are *Symmeria*, *Alchornea*, *Pachira aquatica*, *Mabea*, and *Polypodium* sp. 2.

Diversity measurements were compared between the Holocene environments. The minimum sample coverage obtained was 0.8 (lake margin), so we used that value to perform the coverage-based rarefaction for all Holocene samples. Mean rarefied richness was 22.2 [standard deviation (SD) = 12.6, $n = 12$] for várzea and 26.8 (SD = 28.6, $n = 6$) for lake margin, the difference being non-significant (t-test, $p < 0.7$, df = 6) (Figure 3A). Mean Shannon index was 2.7 for várzea and 2.7 for lake margin palynofloras, the difference being non-significant (t-test, $p < 0.8$, df = 10.2). We also looked at composition similarity between Holocene environments. The mean Chao dissimilarity comparing várzea samples with each other was 0.35 (SD = 0.17, $n = 66$), whereas for lake margin samples it was 0.48 (SD = 0.24, $n = 15$) (Figure 3B). When várzea was compared with lake margin samples (mean = 0.72, SD = 0.12, $n = 72$) the Chao dissimilarity was significantly higher (ANOVA, df = 2, $p < 0.001$) than either within-sample comparison, of várzea or lake margin.

The ecological groups flooded, non-flooded, and flooded/non-flooded have similar abundance proportions between our flooding environments. Várzea has a mean abundance of F of 3.6% (SD = 3.15, $n = 12$), 3.4% for NF (SD = 3.1, $n = 12$) and 71.1% for FNF (SD = 13, $n = 12$). Lake margin has a mean 10.7% F (SD = 7, $n = 6$), 1.2% NF (SD = 1.7, $n = 6$), and 86.2% FNF (SD = 56.7, $n = 6$) (Figure 4A). There is no significant difference in the proportions of F (t-test, df = 6, $p < 0.06$) or NF (t-test, df = 15.54, $p < 0.07$). FNF is higher in várzea environments compared to lake margins (t-test, df = 9.47, $p < 0.05$). In terms of proportional richness, várzea has a mean richness of 3.2% F (SD = 2.1, $n = 12$), 9.3% NF (SD = 3.4, $n = 12$), and 65.6% FNF (SD = 7.2, $n = 12$). Lake margin has a mean 8% F (SD = 5, $n = 6$), 3.7% NF (SD = 3.1, $n = 6$) and 53.8% FNF (SD = 7.1, $n = 6$) (Figure 4B). Várzea has a significantly higher proportion of NF (t-test, df = 11, $p < 0.01$) and FNF (t-test, df = 10.25, $p < 0.01$) compared with lake margin, but the proportion of F is not significantly different (t-test, df = 8.4, $p < 0.07$) (Figure 4B).

4.2. Miocene samples

We found no evidence that our Miocene samples have a taphonomic control or that they captured preferentially one type of forest. First, the nMDS did not indicate that palynological assemblages are controlled by lithofacies (Figure 5A, stress = 0.2). The mean Euclidean distance for within-mudstone samples is 97.7 (SD = 38.1, $n = 16$), for within-siltstone samples it is 83.6 (SD = 27.4, $n = 11$), and for mudstone-siltstone samples it is 88 (SD = 38.8, $n = 27$). There are only two sandstone samples, but they did not cluster together (Figure 5A). The Euclidean distance of mudstone-siltstone comparisons is not significantly different from that of within-siltstone samples (t-test, df = 56.4, $p < 0.3$), but it is significantly higher than that of within-mudstone samples (t-test, df = 166, $p < 0.01$) (Figure 6A). Second, the nMDS did not indicate that palynological assemblages are segregated by type of forest (Figure 5B, stress = 0.2). When comparing the Euclidean distance between

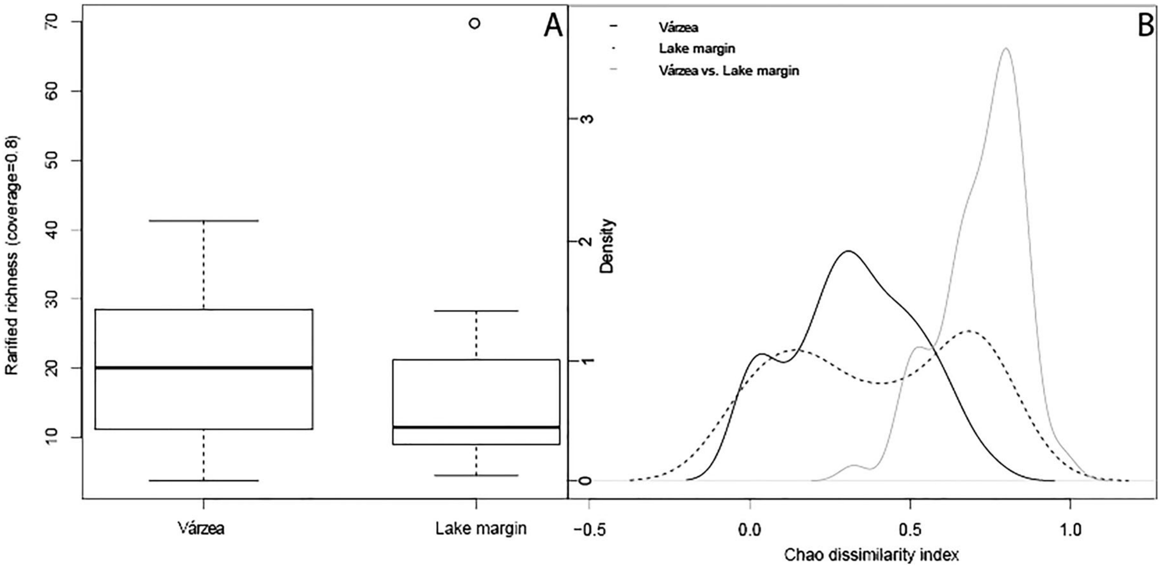

Figure 3. (A) Mean rarefied richness (coverage = 0.8) and (B) mean Chao dissimilarity index for the Holocene flooded environments (várzea and lake margin).

ecological groups (Table 1), the NF group is significantly more clustered than all the other groups (Table 2). The aquatic group is more clustered than the FNF group, which is more clustered than the F group (Table 2; Figure 6B).

Pollen diversity also was not controlled by lithofacies. The lowest sample coverage for the dataset was 0.8, and consequently it was used to perform the coverage-based rarefaction. Mudstone mean rarified richness was 18.7 (SD = 10.7, $n = 16$), that of siltstone was 32.1 (SD = 20.5, $n = 11$), and that of sandstone was 23.9 (SD = 3.5, $n = 2$), the difference being non-significant (t-test mudstone vs. siltstone, df = 30, $p = 1$) (Figure 6C). The mudstone mean Shannon index was 2.5 (SD = 0.5, $n = 16$), that of siltstone was 2.7 (SD = 0.28, $n = 11$), and that of sandstone was 2.9 ($n = 2$), the difference being non-significant (t-test mudstone vs. siltstone, df = 2, $p < 0.1$).

4.3. Holocene versus Miocene comparisons

We found that our Miocene samples are less heterogeneous in pollen composition than those from the Holocene. Miocene samples have a mean dissimilarity Chao index of 0.25 (SD = 0.1, $n = 406$), while for Holocene samples it is 0.5 (SD = 0.2, $n = 171$), and for Holocene versus Miocene it is 0.7 (SD = 0.1, $n = 551$). The Miocene Chao index is significantly lower than the Holocene Chao index (t-test, df = 228.3, $p < 0.001$). The Miocene vs. Holocene Chao index is significantly higher than either the Miocene or Holocene Chao index alone (t-test Miocene, df = 752.1, $p < 0.001$, t-test Holocene, df = 197, $p < 0.001$) (Figure 7B).

We found no difference in pollen diversity between Miocene and Holocene samples. The lowest sample coverage for the entire dataset was 0.8, and consequently it was used to perform the coverage-based rarefaction. The Miocene mean rarefied richness was 20.3 (SD = 12.4, $n = 29$) and that for the Holocene was 20.1 (SD = 15.3, $n = 19$) (Figure 7A), the difference being non-significant (t-test, df = 32.9, $p < 0.9$). T16 richness is not significantly different from Holocene (t-test, df = 23.9, $p < 0.9$), nor is T15 (t-test, df = 3.5, $p < 0.1$), T14 (t-test, df = 7, $p < 0.8$), or T13 (t-test, df = 25.7, $p < 0.1$). Furthermore, the Miocene mean Shannon index was 2.6 (SD = 0.42, $n = 29$) whereas the Holocene value was 2.7 (SD = 0.65, $n = 19$), the difference being non-significant (t-test, df = 28.1, $p < 0.8$). When comparing individual biozones with the Holocene, the Shannon index revealed no significant difference for T16 (t-test, df = 21.9, $p < 0.9$), T15 (t-test, df = 13.5, $p < 0.1$), T14 (t-test, df = 15.2, $p < 0.8$), or T13 (t-test, df = 27.7, $p < 0.1$).

Because the Holocene lithotypes are all mudstones, we ran a diversity comparison using this lithotype only. The lowest sample coverage was, again, 0.8. The Holocene mean rarefied richness was 20.6 (SD = 16, $n = 19$) while that for the Miocene was 16.7 (SD = 9.5, $n = 16$), the difference being non-significant (t-test, df = 30, $p < 0.3$). The Miocene mean Shannon index for mudstone was 2.5 (SD = 0.5, $n = 16$) whereas that for the Holocene was 2.7 (SD = 0.65, $n = 19$), also non-significant (t-test, df = 32.6, $p < 0.4$).

Finally, we noticed sampling saturation was not reached yet. There are 231 morphotypes when all 18 Holocene samples are put together and saturation was not reached (Figure 8). When all 29 Miocene samples are compiled there are a total of 284 morphotypes, and saturation was not reached (Figure 8).

5. Discussion

5.1. Holocene environments

Our analysis indicates that sediments from different environments in western Amazonia have distinct pollen signals (Figure 2A). Samples from várzea are well separated from samples taken along lake margins (Figures 1C–H and 2A). The most abundant types (composing ~70%) differ significantly. In várzea, the most abundant types (Poaceae, *Polypodium* sp. 1, *Polypodium* sp. 2, *Polypodium* sp. 3, and *Microgramma*) are all herbaceous. Várzea is rich in pioneering vegetation, including herbaceous ferns and floating

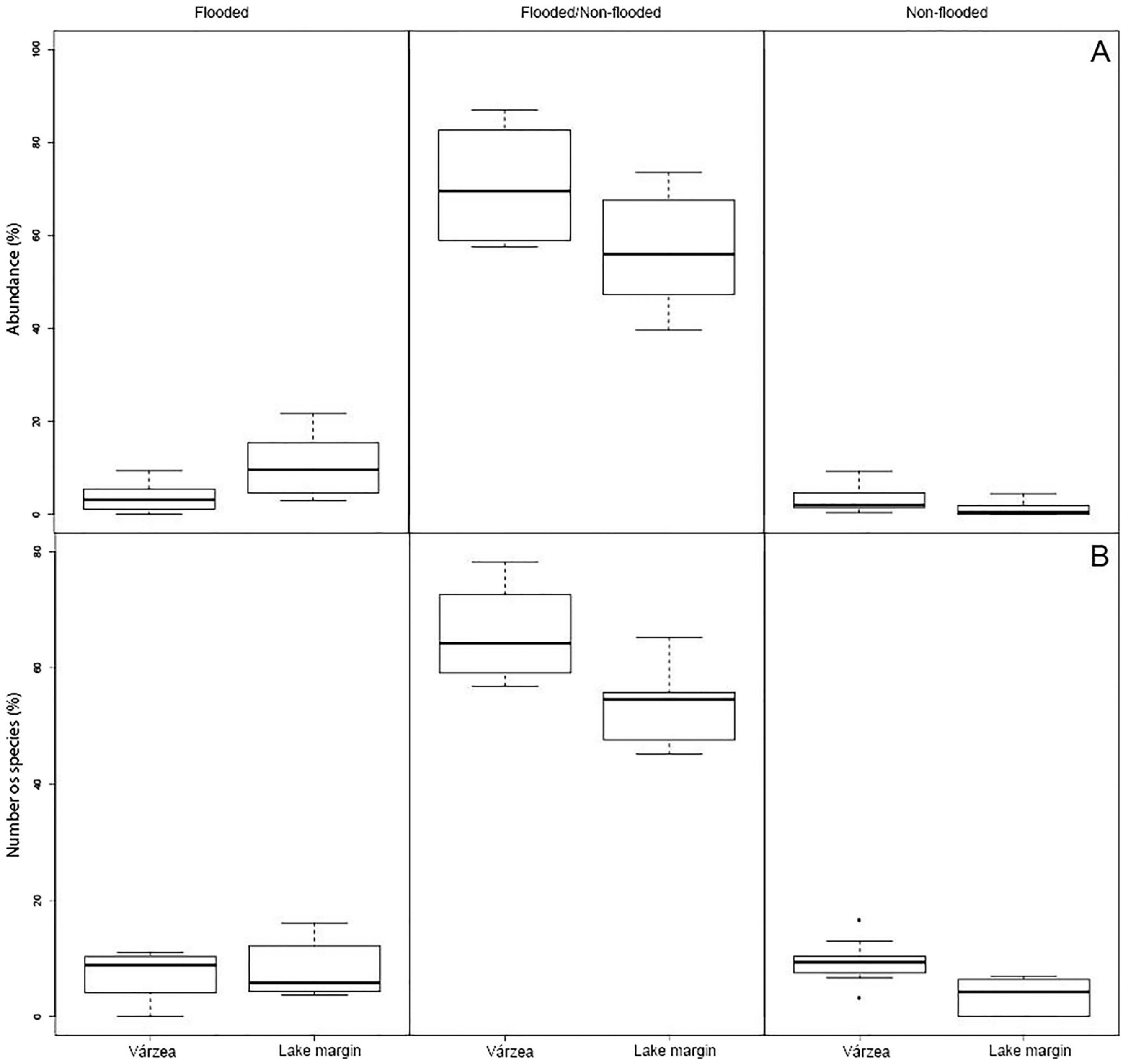

Figure 4. (A) Relative abundance and (B) proportional richness of several ecological groups (flooded, flooded/non-flooded and non-flooded) for Holocene flooded environments (várzea and lake margin).

meadows (Absy 1979; Roucoux et al. 2013), indicating mostly early successional vegetation on bars that are highly dynamic; channel lateral migration in western Amazonia can reach as much as 100–200 m per year (Räsänen et al. 1991). In contrast, except for *Polypodium* sp. 2, the most abundant types in lake margin (*Symmeria*, *Alchornea*, *Pachira aquatica*, *Mabea*, and *Polypodium* sp. 2) are common tree elements in Amazonian floodplains (Wittmann et al. 2004). Pollen assemblages in Pantano de Mónica (middle Caquetá River in Colombia), a marsh not strongly influenced by river flooding dynamics, were also dominated by arboreal taxa and had scarce Poaceae (Behling et al. 1999). These differences could also be explained by distinct pollen dispersal characteristics. For instance, proximity to larger water bodies will lead to more wind-transported taxa such as Poaceae, which was the most abundant type in várzea samples. In contrast, smaller water bodies like the inner-floodplain lakes will collect more of the local vegetation, hence including more local tree elements and less of the herbaceous ones.

Várzea samples are more similar to each other than lake margin samples are to each other (Figure 3B). Our várzea sites are dynamic sedimentary environments, being both flooded for a large portion of the year and heavily affected by lateral migration of bars. In contrast, our lake margin settings are more stable, allowing more stable plant communities. Both várzea and lake margin are dominated by F and FNF taxa (74.7% and 96.9% in abundance, 68.8% and 61.8% in number of taxa, respectively; Figure 4); they contain only a minor proportion of exogenous pollen derived from NF environments (3.4% in abundance and 1.2% in number of taxa; Figure 4), underscoring that both várzea and lake margin samples are dominated by local components rather than an ex-situ

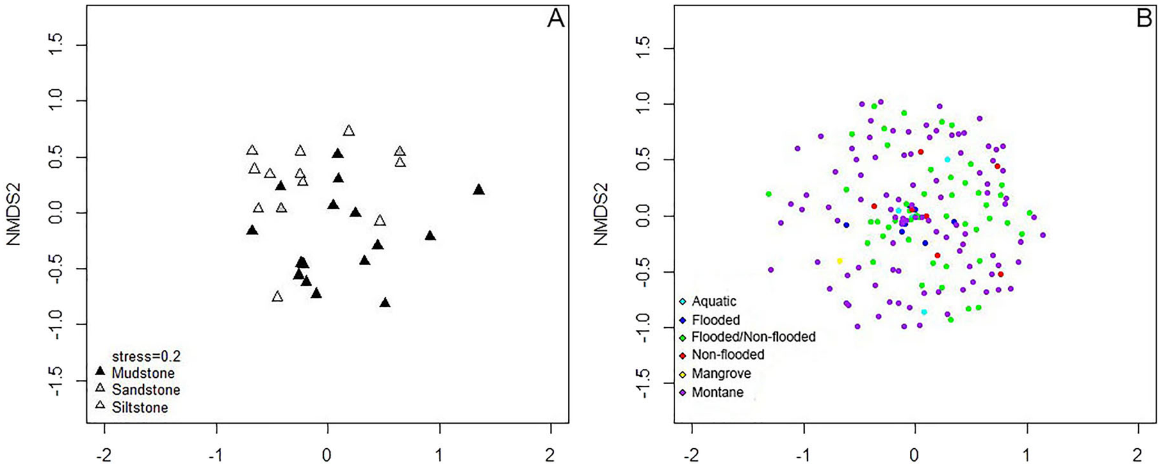

Figure 5. Non-metric multidimensional scaling (nMDS) of the Miocene samples. (A) Samples do not separate along lithofacies (mudstone, silstone, sandstone). (B) Species do not cluster according to ecological preference (aquatic, flooded, flooded/non-flooded, non-flooded, unknown and mangrove).

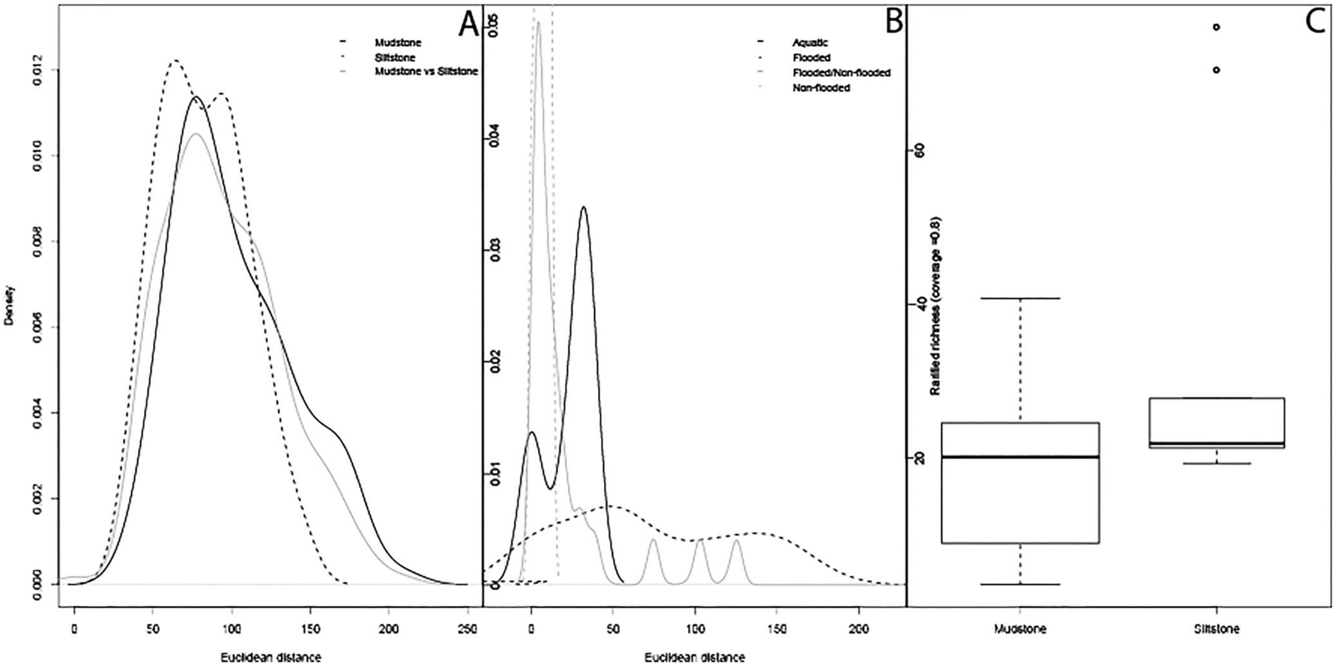

Figure 6. (A) Mean Euclidean distance of the nMDS Miocene lithofacies analysis of Figure 5A (mudstone, silstone). (B) Mean Euclidean distance of the nMDS Miocene ecological analysis of Figure 5B (aquatic, flooded, flooded/non-flooded, non-flooded). (C) Mean rarefied richness (coverage = 0.8) of Miocene lithofacies (mudstone, siltstone, sandstone).

Table 1. Euclidean distance within ecological groups of the Miocene palynoflora.

Group	Euclidean distance
Aquatic	22.80 (SD = 14.3, $n = 16$)
Flooded	73.95 (SD = 54, $n = 64$)
Flooded/Non-flooded	53.7 (SD = 47.9, $n = 56$)
Non-flooded	6.5 (SD = 4, $n = 49$).

SD: standard deviation.

Table 2. T-tests between the mean Euclidian distance within ecological groups of Miocene palynoflora.

t-test	Flooded	Flooded/non-flooded	Non-flooded
Aquatic	$P < 000.1$	$P < 0.008$	$P < 000.1$
Flooded		P < 000.1	P < 000.1
Non-flooded		P < 000.1	

influence. Pollen sourced from Andean areas consists mostly of *Alnus* and represents a minor component of the assemblage (mean of 1.7% in várzea samples and absent from lake margin samples); it was probably transported in the sediment load of the large rivers with headwaters in the Andes.

Várzea forests from western Amazonia (Wittmann et al. 2006) include several of the taxa found in our pollen samples, including Moraceae, *Cecropia*, *Alchornea* sp., *Mabea* sp., Myrtaceae, *Ilex*, *Sapium*, and *Vitex*. *Alchornea* is a pioneer tree on dynamic riverbanks, often forming monospecific stands (Kalliola et al. 1991; Wittmann et al. 2006). *Mabea* and one species of Myrtaceae (*Calyptranthes crebra* McVaugh) are among the important taxa from low várzeas (Wittmann et al. 2006), whereas *Sapium* is an important element in high várzeas. Overall, our pollen spectrum is representative of the flooded forests.

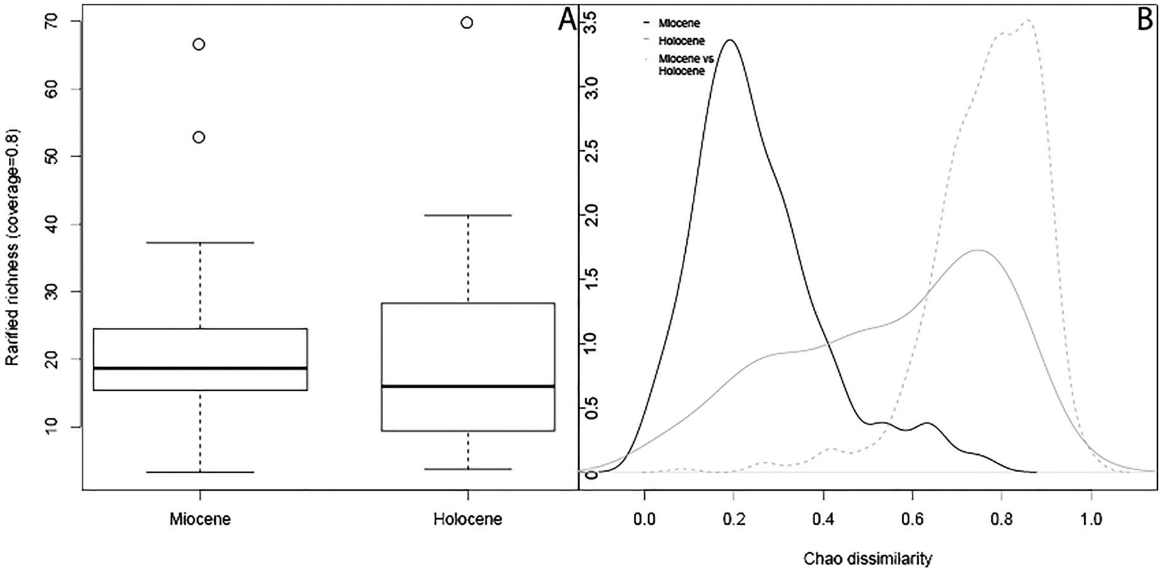

Figure 7. (A) Mean rarefied richness (coverage = 0.8) and (B) mean Chao dissimilarity index for the Miocene and Holocene palynofloras.

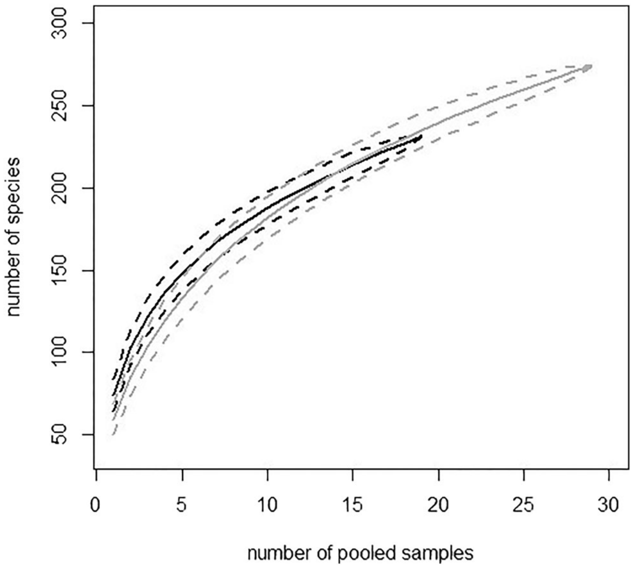

Figure 8. Species accumulation curve for Holocene (black lines) and Miocene (grey lines) samples.

The most important families from floodplains are also found in terra firme forests, with ~30% of species shared (Wittmann et al. 2006). This is reflected in our pollen record, which is dominated by FNF taxa (Figure 4), and similar results were obtained in other studies in the region (e.g. Behling et al. 1999; Roucoux et al. 2013). It is also possible that the large dominance of the FNF group is due to our inability to distinguish species within genera using light microscopy. The development of new instrumental microscopy (e.g. confocal with air-dry scan) could greatly increase the number of measurable pollen morphological traits, thus helping to solve this issue (Sivaguru et al. 2018).

5.2. Holocene versus Miocene comparisons

Both Holocene and Miocene samples are dominated by the FNF and F groups with only a small contribution of the NF group, suggesting that in both sets of samples pollen is primarily sourced from the local, flooded environments. One difference, however, is a small (2.1%) contribution of aquatic plants in the Miocene palynoflora (e.g. *Echiperiporites akanthos*, *Proxapertites psilatus*, *Azolla* sp., and *Hydrosporis minor*) that is absent in the Holocene samples. This difference might be expected given that the modern flooded environment of western Amazonia represents only a small component of the landscape (~20% by area; Toivonen et al. 2007), whereas it was extensive during the time of the Pebas System.

There was no difference in within-sample diversity between Holocene and Miocene palynofloras. The comparison, however, is not straightforward, as the core sampled the same geographical position across geological time and a variety of depositional settings, whereas the Holocene samples represent the same time slice across multiple geographical positions. It is possible that the lack of difference is driven by the nature of the flooded environments, as similar environments are sampled in both the Miocene and Holocene. To address this concern, it would be necessary to include in the analysis samples from non-flooded settings, from both the Miocene and the Holocene, to compare and contrast with the flooded environments.

A surprising result was that the Holocene samples were more heterogeneous relative to each other than were the Miocene samples relative to each other (Figure 7B). Given that Miocene samples span millions of years and a larger variety of depositional settings than the Holocene samples, the opposite pattern would be expected. We hypothesize that the Pebas System was highly homogeneous at a continental scale, much more so than modern western Amazonia, thus suggesting that the spatial vegetation turnover was much lower than in modern ecosystems. We need a much more extensive geographical sampling of the Pebas System to test this hypothesis, but this could lead to a number of future research questions, including: (1) where did the non-flooded taxa come from (e.g. Eastern Amazonia)?; (2) was the extant high diversity of non-flooded habitats (e.g. terra firme) developed over the past 8–9 million years?; and (3) are there large extinctions of plant clades associated with the Miocene flooded environments of the Pebas System?

Western Amazonia is a continental-scale area holding the greatest plant biodiversity in the world. We are still in the early stages of understanding its evolution, but without doubt, the fossil record holds the key to unraveling one of the oldest questions in evolutionary science: Why are the tropics so diverse?

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References

A Morphological Electronic Database of Cretaceous–Tertiary and Extant pollen and spores from Northern South America 2014. Panamá: Smithsonian Tropical Research Institute. [updated 2019 Jan 1, accessed 2019 Jan 15]. http://biogeodb.stri.si.edu/jaramillo/palynomorph/.

Absy ML. 1979. A palynological study of the Holocene sediments in the Amazon Basin [dissertation]. Amsterdam: University of Amsterdam.

Antonelli A, Zizka A, Carvalho FA, Scharn R, Bacon CD, Silvestro D, Condamine FL. 2018. Amazonia is the primary source of Neotropical biodiversity. Proceedings of the National Academy of Sciences. 115(23):6034–6039.

Antonelli A, Zizka A, Silvestro D, Scharn R, Cascales-Miñana B, Bacon CD. 2015. An engine for global plant diversity: highest evolutionary turnover and emigration in the American tropics. Frontiers in Genetics. 6(130):1–14.

Behling H, Berrío JC, Hooghiemstra H. 1999. Late Quaternary pollen records from the middle Caquetá river basin in central Colombian Amazon. Palaeogeography, Palaeoclimatology, Palaeoecology. 145(1–3):193–213.

Behling H, Bush M, Hooghiemstra H. 2010. Biotic development of Quaternary Amazonia: a palynological perspective. In Hoorn MC, Wesselingh FP, editors. Amazonia, landscape and species evolution: a look into the past. Oxford: Wiley-Blackwell Publishing; p. 335–345.

Bernal R, Bacon CD, Balslev H, Hoorn C, Bourlat SJ, Tuomisto H, Salamanca S, Manen MT, Romero I, Sepulchre P, Antonelli A. 2019. Could coastal plants in western Amazonia be relicts of past marine incursions? Journal of Biogeography. 46(8):1749–1759.

Boonstra M, Ramos MIF, Lammertsma EI, 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.

Caputo MV, Soares E. 2016. Eustatic and tectonic change effects in the reversion of the transcontinental Amazon River drainage system. Brazilian Journal of Geology. 46(2):301–328.

Chao A, Chazdon RL, Colwell RK, Shen T-J. 2004. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters. 8(2):148–159.

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology. 93(12):2533–2547.

Colinvaux P, Oliveira PE, Patiño J. 1999. Manual e Atlas palinológico da Amazônia. Amsterdam (NH): Harwood Academic Publishers.

Cruz N. 1984. Palinologia do Linhito do Solimões no Estado do Amazonas. Paper presented at: Anais do II Simpósio Amazônico; Manaus (AM). 7p.

D'Apolito C. 2016. Landscape evolution in Western Amazonia: palynostratigraphy, palaeoenvironments and diversity of the Miocene Solimões Formation, Brazil [dissertation]. Birmingham: School of Geography, Earth and Environmental Sciences College of Life and Environmental Sciences/University of Birmingham.

D'Apolito C, Da Silva-Caminha SA, Jaramillo C, Dino R, Soares E. 2019. The Pliocene–Pleistocene palynology of the Negro River, Brazil. Palynology. 43:223–243.

Deng C, Daley T, Smith AD. 2015. Applications of species accumulation curves in large-scale biological data analysis. Quantitative Biology. 3(3):135–144.

Edwards LE. 1989. Supplemented graphic correlation: a powerful tool for paleontologists and nonpaleontologists. Palaios. 4(2):127–143.

Eiras JF, Becker CR, Souza EM, Gonzaga FG, Silva JGF, Daniel LMF, Matsuda NS, Feijó FJ. 1994. Bacia do Solimões. Boletim de Geociências da Petrobrás. 8:17–45.

Erdtman G. 1952. Pollen morphology and plant taxonomy - angiosperms: an introduction to palynology. Stockholm: Almqvist & Wiksell.

Faegri K, Iversen J. 1966. Textbook of modern pollen analysis. Copenhagen: Ejner Munksgaard.

Figueiredo J, Hoorn C, van der Ven P, Soares E. 2009. Late Miocene onset of the Amazon River and the Amazon deep-sea fan: evidence from the Foz do Amazonas basin. Geology. 37(7):619–622.

Germeraad JH, Hopping CA, Muller J. 1968. Palynology of Tertiary sediments from tropical areas. Review of Palaeobotany and Palynology. 6(3-4):189–348.

Gordon A. 1999. Classification. London: Chapman and Hall/CRC Press.

Google Earth Pro. 2019. Release 7.3.2.5776. California: Google LLC.

Hooghiemstra H, Van Der Hammen T. 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. Earth-Science Reviews. 44(3-4): 147–183.

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(3/4):267–309.

Hoorn C. 1994a. An environmental reconstruction of the palaeo-Amazon River system (Middle to Late Miocene, NW Amazonia). Palaeogeography, Palaeoclimatology, Palaeoecology. 112(3-4): 187–238.

Hoorn C. 1994b. Fluvial palaeoenvironments in the intracratonic Amazonas Basin (Early Miocene-early Middle Miocene, Colombia). Palaeogeography, Palaeoclimatology, Palaeoecology. 109(1):1–54.

Hoorn C. 2006. Mangrove forests and marine incursions in Neogene Amazonia (Lower Apaporis River, Colombia). Palaios. 21(2):197–209.

Hoorn C, Bogotá ARG, Romero-Baez M, Lammertsma EI, Flantua S, Dantas EL, Dino R, Do Carmo DA, Chemale JF. 2017. The Amazon at sea: Onset and stages of the Amazon River from a marine record in the Foz do Amazonas Basin (Brazilian Equatorial Margin), with special reference to vegetation turnover in the Plio-Pleistocene. Global and Planetary Change. 153:51–65.

Hoorn C, van der Ham R, de la Parra F, Salamanca S, ter Steege H, Banks H, Star W, van Heuven BJ, Langelaan R, Carvalho FA, et al. 2019. Going north and south: The biogeographic history of two Malvaceae in the wake of Neogene Andean uplift and connectivity between the Americas. Review of Palaeobotany and Palynology. 264:90–109.

Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartin I, Sanchez-Meseguer A, Anderson CL, Figueiredo JP, et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. Science. 330(6006):927–931.

Hsieh TC, Ma KH, Chao A. 2018. iNEXT: iNterpolation and EXTrapolation for species diversity. R Package Version. 2018

IBGE 1977. Folha SB-19 Juruá. Rio de Janeiro (RJ): Instituto Brasileiro de Geografia e Estatística.

Jaramillo CA, Hoorn C, Silva SAF, Leite F, Herrera F, Quiroz L, Dino R, Antonioli L. 2010a. The origin of the modern Amazon rainforest: implications of the palynological and palaeobotanical record. In: Hoorn MC and Wesselingh FP, editors. Amazonia, Landscape and Species Evolution: A Look into the Past. Oxford: Wiley-Blackwell Publishing; p. 317–334.

Jaramillo CA, Rueda JM, Mora G. 2006. Cenozoic plant diversity in the neotropics. Science. 311(5769):1893–1896.

Jaramillo CA, Rueda M, Vladimir T. 2011. A palynological zonation for the Cenozoic of the Llanos and Llanos Foothills of Colombia. Palynology. 35(1):46–84.

Jaramillo C, Romero I, D'Apolito C, Bayona G, Duarte E, Louwye S, Escobar J, Luque J, Carrillo-Briceño JD, Zapata V, et al. 2017. Miocene flooding events of western Amazonia. Science Advances. 3(5): e1601693.

Junk WJ. 1997. General aspects of floodplain ecology with special reference to Amazonian floodplains. In: Junk WJ, editor. The central Amazon floodplain: ecology of a pulsating system. Vol. 126. Berlin: Springer; p.3–22.

Junk WJ. 1992. Wetlands of tropical South America. In: Whigham DF, Dykyjova D, Hejny S, editors. Wetlands of the World. Vol. 1. Dordrecht: Junk Publishers; p. 679–739.

Junk WJ, Piedade MTF, Schöngart J, Wittmann F. 2012. A classification of major natural habitats of Amazonian white-water river floodplains (varzeas). Wetlands Ecology and Management. 20(6):461–475.

Kachinasz KR, Silva-Caminha S. 2016. Palinoestratigrafia da Formação Solimões: comparação entre bioestratigrafia tradicional e o método de associações unitárias. Revista Brasileira de Paleontologia. 19(3): 481–490.

Kalliola R, Salo J, Puhakka M, Rajasilta M. 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. The Journal of Ecology. 79(4):877–901.

Kummel B, Raup D. 1965. Handbook of paleontological techniques. San Francisco (CA): Freeman.

Latrubesse EM, Cozzuol M, Silva-Caminha SAF, Rigsby CA, Absy ML, Jaramillo C. 2010. The late Miocene paleogeography of the Amazon basin and the evolution of the Amazon River system. Earth-Science Reviews. 99(3–4):99–124.

Leite FPR, Paz J, do Carmo DA, Silva-Caminha SA. 2017. The effects of the inception of Amazonian transcontinental drainage during the Neogene on the landscape and vegetation of the Solimões Basin, Brazil. Palynology. 41(3):412–422.

Linhares AP, Gaia VS, Ramos M. 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.

Lorente FL, Junior AAB, Oliveira PE, Pessenda L. 2017. Atlas palinologico: laboratório ^{14}C-Cena/USP. Piracicaba: FEALQ.

Lorente MA. 1986. Palynology and palynofacies of the Upper Tertiary in Venezuela. Stuttgart: Dissertationes Botanicae.

Magurran AE. 2004. Measuring biological diversity. Oxford: Blackwell Science.

Maia RG, Godoy HK, Yamaguti HS, Moura PA, Costa FS, Holanda MA, Costa J. 1977. Projeto de carvão no Alto Solimões. Manaus: DNPM/CPRM.

Maia MAM, Marmos JL. 2010. Geodiversidade do estado do Amazonas. Manaus: CPRM.

Muller J, Giacomo E, Van Erve AW. 1987. A palynological zonation for the Cretaceous, Tertiary, and Quaternary of northern South America. American Association of Stratigraphic Palynologists Contributions Series, No. 19, 76 p.

Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR. 2017. Vegan: community ecology package. [accessed 2019 Jan 15]. https://CRAN.R-project.org/package=vegan.

Parolin P, Oliveira AC, Piedade MTF, Wittman F, Junk WJ. 2002. Pioneer trees in Amazonian floodplains: key species form monospecific stands in different habitats. Folia Geobotanica. 37(2):225–238.

Pennington RT, Dick CW. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences. 359(1450):1611–1622.

Prance GT. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia. 3: 26–38.

R Development Core Team. 2018. R: A language and environment for statistical computing. Release 3.4.2. Vienna: R Foundation for Statistical Computing.

Räsänen ME, Salo JS, Jungner H. 1991. Holocene floodplain lake sediments in the Amazon: ^{14}C dating and paleoecological use. Quaternary Science Reviews. 10(4):363–372.

Regali MS, Uesegui N, Santos A. 1974. Palinologia dos sedimentos Meso–Cenozoicos do Brasil (I). Boletim Técnico da Petrobrás. 17: 263–362.

Ricklefs RE, Renner SS. 2012. Global correlations in tropical tree species richness and abundance reject neutrality. Science. 335(6067):464–467.

Roubik DW, Moreno JE. 1991. Pollen and spores of Barro Colorado Island. St. Louis (MO): Missouri Botanical Garden.

Roucoux KH, Lawson IT, Jones TD, Baker TR, Coronado EN, Gosling WD, Lähteenoja O. 2013. Vegetation development in an Amazonian peatland. Palaeogeography, Palaeoclimatology, Palaeoecology. 374: 242–255.

Salamanca S, van Soelen E, Teunissen ML, Flantua S, Ventura-Santos R, Roddaz M, Dantas EL, van Loon E, Sinninghe Damsté JS, Kim J-H, Hoorn C. 2016. Amazon forest dynamics under changing abiotic conditions in the early Miocene (Colombian Amazonia). Journal of Biogeography. 43(12):2424–2437.

Shephard GE, Müller RD, Liu L, Gurnis M. 2010. Miocene drainage reversal of the Amazon River driven by plate–mantle interaction. Nature Geoscience. 3(12):870–875.

Silva-Caminha SAF, Jaramillo C, Absy ML. 2010. Neogene palynology of the Solimões Basin, Brazilian Amazonia. Palaeontographica Abteilung B. 283:1–67.

Silveira RR, Souza PA. 2015. Palinologia (grãos de pólen de angiospermas) das formações Solimões e Içá (bacia do Solimões), nas regiões de Coari e Alto Solimões, Amazonas. Revista Brasileira de Paleontologia. 18(3):455–474.

Silveira RR, Souza PA. 2016. Palinologia (esporos de fungos e pteridófitas, grãos de pólens de gimnospermas, cistos de algas e escolecodonte) das formações Solimões e Içá (Neogeno e Pleistoceno, Bacia do Solimões), Amazonas, Brasil. Pesquisas em Geociências. 43(1):17–39.

Silveira RR, Souza PA. 2017. Palinoestratigrafia da Formação Solimões na Região do Alto Solimões (Atalaia do Norte e Tabatinga), Amazonas, Brasil. Geosciences = Geociências. 36(1):100–117.

Sivaguru M, Urban MA, Fried G, Wesseln CJ, Mander L, Punyasena SW. 2018. Comparative performance of airyscan and structured illumination superresolution microscopy in the study of the surface texture and 3D shape of pollen. Microscopy Research and Technique. 81(2): 101–114.

Thomas WW. 1999. Conservation and monographic research on the flora of tropical America. Biodiversity and Conservation. 8(8):1007–1015.

Toivonen T, Maki S, Kalliola R. 2007. The riverscape of Western Amazonia – A quantitative approach to the fluvial biogeography of the region. Journal of Biogeography. 34(8):1374–1387.

Urrego LE. 1994. Los bosques inundables del Medio Caqueta (Amazonia Colombiana): caracterizacion y sucesión [dissertation]. Amsterdam: University of Amsterdam.

Van Der Hammen T, Hooghiemstra H. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. Quaternary Science Reviews. 19(8):725–742.

Van der Hammen T. 1954. The development of Colombian flora throughout geologic periods: I, Maestrichtian to Lower Tertiary. Boletín Geológico. 2:49–106.

Wesselingh FP. 2006. Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia. Scripta Geologica. 133:19–290.

Wesselingh FP, Räsänen ME, Irion G, Vonhof HB, Kaandorp R, Renema W, Romero PL, Gingras M. 2002. Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western. Amazonia. Cenozoic Research. 1:35–81.

Wing SL, Herrera F, Jaramillo CA, Gómez-Navarro C, Wilf P, Labandeira CC. 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. Proceedings of the National Academy of Sciences. 106(44): 18627–18632.

Wittmann F, Junk WJ, Piedade M. 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. Forest Ecology and Management. 196(2-3): 199–212.

Wittmann F, Schöngart J, Montero JC, Motzer T, Junk WJ, Piedade MTF, Queiroz HL, Worbes M. 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. Journal of Biogeography. 33(8):1334–1347.

Wittmann F, Anhuf D, Funk WJ. 2002. Tree species distribution and community structure of Central Amazonian várzea forests by remote sensing techiniques. Journal of Tropical Ecology. 18(6):805–820.

Wood GD, Gabriel AM, Lawson JC. 1996. Palynological techniques-processing and microscopy. In: Jansonius J, McGregor DC, editors. Palynology, principles and applications. Dallas (TX): American Association of Stratigraphic Palynologists Foundation; p. 29–50.