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Late Quaternary vegetation dynamics from central parts of the Madeira River in Brazil

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ABSTRACT

The present study reconstructs the paleovegetation of a varzea (seasonally flooded) forest in the central parts of the Madeira River floodplain in Brazil using palynological data. Forty-nine cut-bank sediment samples from the Madeira River were processed in the study; from these, ten samples contained pollen: two contained pollen from the Middle Pleniglacial age, one contained pollen from the Tardiglacial age, six contained pollen from the Holocene, and one contained more recently deposited pollen. The Middle Pleniglacial pollen belonged to a primary succession varzea forest, while the Tardiglacial pollen represented a late succession varzea forest. On the other hand, the three Holocene samples showed the characteristic composition of chavascal (water-logged forest) or lacustrine varzea forest, and three samples belonged to a late succession varzea forest. The most recent pollen deposit represented a secondary succession varzea forest. This paleovegetation showed a typical mosaic distribution, which may be explained by the fluvial dynamics, high species richness and diversity in the varzea forest, and the presence of dominant species.

Keywords: Cut-bank sediment, late Pleistocene–Holocene, palynology, southern Amazonian tributary, varzea

Introduction

Palynological studies have played a crucial role in the reconstruction of past vegetation (Absy *et al*. 1991; Hoorn 1997; Mayle *et al*. 2000; Colinvaux *et al*. 2001; D'Apolito *et al*. 2013). However, there are still large gaps in palynological and past vegetation knowledge at different scales. In particular, vast areas of the Amazon region remain unexplored, although several vegetation maps for the last glacial period have been constructed despite this deficiency (Hammen & Absy 1994; Bush 1994; Hooghiemstra & Hammen 1998; Haberle & Maslin 1999; Thomas 2000; Cowling *et al*. 2001; Anhuf *et al*. 2006). These maps show a clear trend of forest retreat following a decrease in rainfall; however, most palynological studies have been conducted in "terra firme" (non-flooded) forests. On the other hand, studies including Quaternary fluvial records have suggested that the Amazon basin experienced a series of paleohydrological changes during the last glacial period (Latrubesse 2003; Latrubesse *et al*. 2005).

The flooded areas within the Amazon basin extend over an area of approximately 30% of the total basin area and include seasonally flooded areas, permanently flooded areas, river mouth areas, and occasionally flooded areas (Junk *et al*. 2011). From these, varzea forests are seasonally flooded by white-water rivers rich in nutrients (Prance 1979) and present the highest plant species richness among all flooded forests worldwide (Wittmann *et al*. 2006); however, little is known of its paleovegetation. Thus, sediments of alluvial terraces from the areas of varzea forest have been collected to reconstruct the vegetation from palynological records for the Amazon River near Manaus, Terra Nova in the Careiro Island, and Caquetá River in the Columbian Amazon (Absy 1979; Hammen *et al*. 1992).

The Madeira River is the world's fourth largest in liquid flow with a drainage basin of 1,300,000 km² (Latrubesse 2008). It is the most important tributary of the Amazon River, accounting for 15% of the Amazon's discharge and providing the greatest contribution of suspended sediments (Goulding *et al*. 2003, Latrubesse *et al*. 2005; Filizola & Guyot 2009). Despite the regional importance of the Madeira River, few paleoecological studies have been conducted on this region. Geological (Latrubesse 2002) and palynological (Absy & Hammen 1976; Hammen & Absy 1994) evidence have showed that the Late Quaternary regional climate was characterized by a series of drier periods. To this end, paly-

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nological evidence from fluvial sediments could provide a more direct reconstruction of the vegetation in the Madeira River region during this period; however, such studies, particularly regarding the Madeira River floodplain have not yet been conducted.

This study aims to reconstruct the paleovegetation of the varzea forest in the central parts of the Madeira River floodplain through palynological analyses and radiocarbon ^{14}C dating from alluvial terrace sediments of the river to contextualise the region within the Amazonian paleoecological setting.

Study area

The study area is located between the cities of Porto Velho and Huimatá (Fig. 1). It presents a characteristic tropical monsoon climate (Am, according to Köppen's climate classification), an average annual temperature of 28°C, and an average rainfall of 2,500–3,000 mm/year (DNPM 1978).

The Madeira River originates in Bolivia from the confluence of the Guaporé, Mamoré, Beni, and Madre de Dios rivers. Approximately 50% of the Madeira River drainage basin is located in Peru (10%) and Brazil (40%). The river drains the Andes Mountain Range, Brazilian Shield, and Amazon Floodplain (Goulding *et al.* 2003; Filizola & Guyot 2009) and develops into a meandering-channel fluvial pattern within the Brazilian territory (Latrubesse 2008; 2012).

Materials and methods

A total of 49 samples from 22 locations were collected from cut banks of different morphostratigraphic units along the Madeira River (sediments from different fluvial terraces; Fig. 1). The material preparation complied with the following phases: sample treatment for 10 minutes in a 10% aqueous solution of potassium hydroxide (KOH) (Faegri & Iversen 1966), followed by acetolysis (Erdtman 1960) and gravity separation using a bromoform-alcohol mixture at a density of 2.0'' (Kummel & Raupp 1965). After gravity separation, the residual material was mounted on glycerinated gelatine slides for optical microscope analysis.

After preparing the slides, the microscopic analysis showed that only 10 samples contained pollen. A total of 300 pollen grains were counted in each analysed sample. Simultaneously, pterydophytae spores were counted stopping when a total of 300 pollen grains was reached. Pteridophyte spores were separated into different morphotypes and identified when possible. To estimate pollen concentration, we added a known number of spores of the exotic species *Lycopodium clavatum* (Stockmar, 1971) to the sample; however, the low number of Lycopodium spores subsequently found in the samples made it impossible to accurately estimate pollen concentration. Pteridophyte spores were not included in the pollen sum. They were separated into different morphotypes, and the percentage of each type of

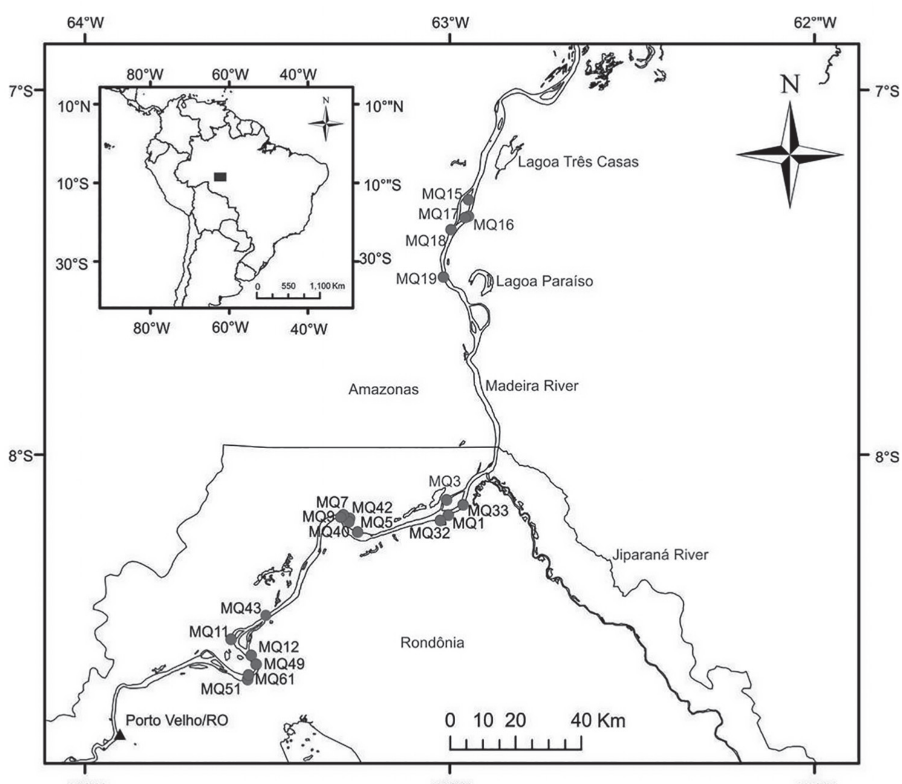

Figure 1: Study area and location where the samples were collected. Location MQ 19 falls within Humaitá city boundaries.

spore was calculated from the sum of pollen. These data were used to draw a pollen diagram for all the study sites whose samples contained pollen.

All pollen was additionally characterized according to type, based on morphological entities encompassing one or more species as taxonomic entities (Joosten & Klerk 2002; Klerk & Joosten 2007). Pollen types were identified from illustrations and descriptions from studies published by Absy (1979), Hooghiemstra (1984), and Roubik & Moreno (1991), and through a comparison with the reference collections held by the Laboratory of Palynology at the National Institute for Amazonian Research (Instituto Nacional de Pesquisas da Amazônia, INPA).

Because the samples are spread over different morphostratigraphic units of the Madeira River, the palynological data obtained are also distributed over time and space. Palynological researches generally focused on a single point and describe how the vegetation on site changed over time. In this case, it is not possible to adopt this methodology, because the differences found between the results of these samples can be derived from different times and places. Therefore, we focused on the description of the vegetation structure. Species dominance is one of the most important structural characteristics in tropical forests (Hart *et al.* 1989). Here we aimed to describe species dominance in the paleovegetation present in the study area; to this end, pollen types were classified according to their frequencies as follows: dominant pollen (>45%), accessory pollen (15% ≤ 45%), rare pollen (3% ≤ 15%), and sporadic pollen (<3%), following the categories for melissopalynology proposed by Louveaux *et al.* (1978).

The Shannon-Weiner diversity index (H) was used to characterise the diversity of the different pollen types. To calculate H, pollen types were grouped into genus whenever possible; however, for families such as Poaceae, Cyperaceae and Moraceae whose identification to genus level is difficult, the types were grouped at the family level. These data was analyzed using un-weighted pair group method with arithmetic mean (UPGMA) analysis.. To minimize the noise, sporadic pollen types from all samples were excluded from the analysis. In addition, the raw data matrix was square root transformed. Cluster analysis, along the pollen diagram and the classification of pollen types based on their frequencies, were used to differentiate the vegetation represented in the pollen record.

The description of paleovegetation of the varzea forest in the central region of the Madeira River followed that of Wittmann *et al.* (2010), which at the same time was based on Worbes *et al.* (1992) and Ayres (1993), with additional data by Schöngart *et al.* (2003) and Wittmann *et al.* (2002; 2004). The aforementioned studies were focused on the central Amazon varzea forests of the Amazon-Solimões River; however, due to the lack of studies focused on varzea forest vegetation of the Madeira River, we adopted these concepts for this study.

Furthermore, samples were selected for analysis by radiocarbon ^{14}C (Tab. 1) at the Centre for Applied Isotope Studies (CAIS, University of Georgia) and Beta Analytic Laboratory. All sample ages were calibrated using the INTCAL13/MARINE13 dataset (Reimer *et al.* 2013).

Results

Among the 49 samples processed, only 10 samples from 8 different locations contained pollen (Tab. 2). The cluster analysis showed four different groups of samples (Fig. 2). These results, together with the pollen diagram (Fig. 3) and the classification of pollen types, allowed us to differentiate the following types of varzea forest: primary succession varzea forest, secondary succession varzea forest, late succession varzea forest, and lacustrine varzea forest or chavascal (Tab. 3).

Location MQ 7 showed a profile with seven lithostratigraphic units (Fig. 4). From this location, we processed samples MQ 7(1), MQ 7(2), MQ 7(4), and MQ 7(5) although pollen was observed only in sample MQ 7(2). Sample MQ 7(2) was from a unit presenting medium gray mud with plane-parallel wavy lamination and sandy inter-layers. Its estimated age was 36,335-34,750 cal ka BP. The sample did not present a dominant pollen type, and Moraceae and *Symmeria* appeared as accessory pollen types. This pollen record suggested the presence of a primary succession varzea forest.

At the location MQ 42, only the MQ 42(1) sample was processed, and its age was estimated to be 28,685–28,195 cal ka BP. Its profile presented four lithostratigraphic units (Fig. 4). The sample was specifically collected was clayey-sandy,

Table 1. Radiometric dating (^{14}C AMS) of cut-bank samples from the middle Madeira River.

Sample	Dated material	Conventional Age (^{14}C years BP)	Calibrated Age (cal year BP)	Laboratory Number
MQ 3(1)	Wood	3,710 ± 20	2,131-2,085	CAIS - 11644
MQ 5(4)	Wood	4,350 ± 25	3,001-2,993	CAIS - 11645
MQ 7(2)	Sediment	33,250 ± 210	28,685-28,195	Beta - 377672
MQ 11(3)	Wood	2,460 ± 20	536-527	CAIS - 11646
MQ 32(1)	Wood	120 ± 20	1,711-1,719	CAIS - 114221
MQ 42(1)	Sediment	26,050 ±100	36,335-34,750	Beta-377673

Table 2. Location and processed samples.

Location	Processed samples
MQ 1	MQ (1)
MQ 3	**MQ 3(1)**, MQ 3(2), MQ 3(3), MQ 3(4), MQ 3(5)
MQ 5	MQ 5(1), **MQ 5(2)**, MQ 5(3), MQ 5(4)
MQ 7	MQ 7(1), **MQ 7(2)**, MQ 7(4), MQ 7(5)
MQ 9	MQ 9(1), MQ 9(2)
MQ 11	MQ 11(1), MQ 11(2), **MQ 11(3)**, **MQ 11(4)**, **MQ 11(5)**, MQ 11(6), MQ 11(7)
MQ 12	MQ 12(1), MQ 12(4), MQ 12(5), MQ 12(6)
MQ 15	MQ 15(1)
MQ 16	MQ 16(1), **MQ 16(2)**
MQ 17	MQ 17(2)
MQ 18	MQ 18(1), MQ 18(5)
MQ 19	MQ 19(1), MQ 19(2)
MQ 32	MQ 32(2)
MQ 33	MQ 33(1), MQ 33(3)
MQ 40	MQ 40(1)
MQ 42	MQ 42(1)
MQ 43	MQ 43(1), MQ 43(2), MQ 43(3)
MQ 49	MQ 49(1), MQ 49(2), MQ 49(3), MQ 49(5)
MQ 51	MQ 51(7), MQ 51(8)
MQ 61	MQ 61(3)

Pollen occurred in the samples in bold.

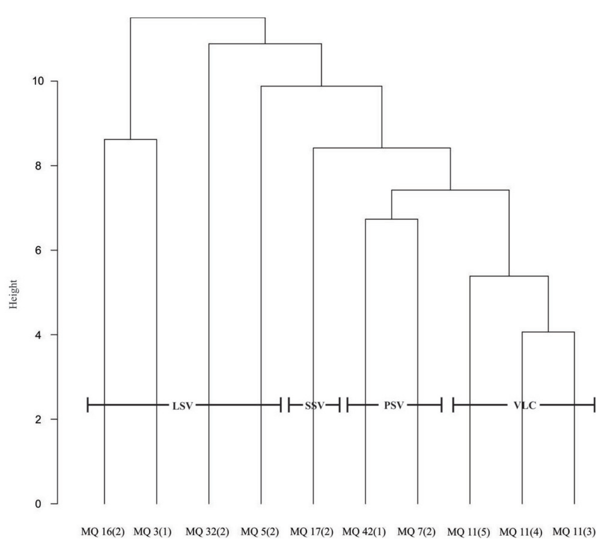

Figure 2. Cluster analysis using Un-weighted Pair Group Method with Arithmetic Mean (UPGMA) analysis. PSV: primary succession varzea; SSV: secondary succession varzea; LSV: Late succession varzea; VLC: lacustrine varzea forest or chavascal.

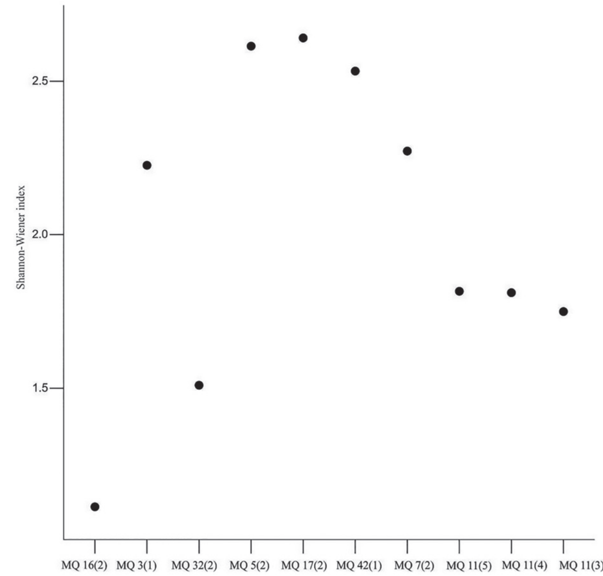

Figure 3. Shannon diversity index of the samples containing pollen.

yellow-cream, laminated, and rippled silt unit. Cyperaceae and Poaceae pollen types appeared as accessory pollen, and no dominant pollen type occurred in MQ 42(1). This pollen assemblage suggested the presence of as primary succession varzea forest on this location in the past.

MQ 16 was located in a morphostratigraphic unit intermediate between a recent plain during the Holocene and a Late Pleistocene unit possibly from the Tardiglacial period. However, further information is required to confirm the age of the unit. From this location, we processed samples MQ 16(1) and MQ 16(2), although we only found pollen in sample MQ 16(2). The profile of this location showed three lithostratigraphic units (Fig. 4); MQ 16(2) was collected from a unit consisting of very fine and muddy sand with incipient lamination and apparent fluidisation, showing the characteristics of a channel. *Sapium* was the dominant pollen type and *Ilex* appeared as accessory pollen in the sample. This assemblage suggested the presence of a late succession varzea forest on this location.

Three samples were processed in location MQ 5: MQ 5(1), MQ 5(2), and MQ 5(3); however, we only found pollen in MQ 5(2). The profile of this location presented four lithostratigraphic units (Fig. 4); MQ 5(2) was collected from a unit consisting of dark gray massive clay rich in leaves and trunks. Moraceae appeared as accessory pollen, and no dominant pollen was detected. This assemblage suggested the presence of a late succession varzea forest on this location. Sample MQ 5(4) was not processed for palynological analysis and used for radiocarbon dating. The age of this sample was estimated to be 3,001–2,993 cal ka BP.

In the MQ 32 location, only MQ 32(2) was processed for palynological analyses. This location presented two lithostratigraphic units, a point bar and scroll bar sequence (Fig. 4). MQ 32(1) was chosen for radiocarbon dating and was collected from a height of 7 m. Its age was estimated

Table 3. Vegetation types present in the pollen record of the Madeira River, vegetation characteristics and dominant and accessory pollen

Vegetation	Samples	Paleovegetation	Dominant and accessory pollen
Primary succession forest	MQ 7(2), MQ 42(1)	Open with monospecific groups of pioneer trees	Cyperaceae, Moraceae, Poaceae and *Symmeria*
Secondary succession forest	MQ 17(2)	Low density with early stratification processes	Melastomataceae
Late succession forest	MQ 5(2), MQ 16(2), MQ 32(2) and MQ 35(1)	Well stratified, high species diversity and richness	Moraceae, *Ilex*, *Sapium* and Euphorbiaceae type 1
Varzea forest of lake or chavascal	MQ 11(3), MQ 11(4), MQ 11(5)	Dense and poor in species	*Alchornea*, Cyperaceae and Moraceae

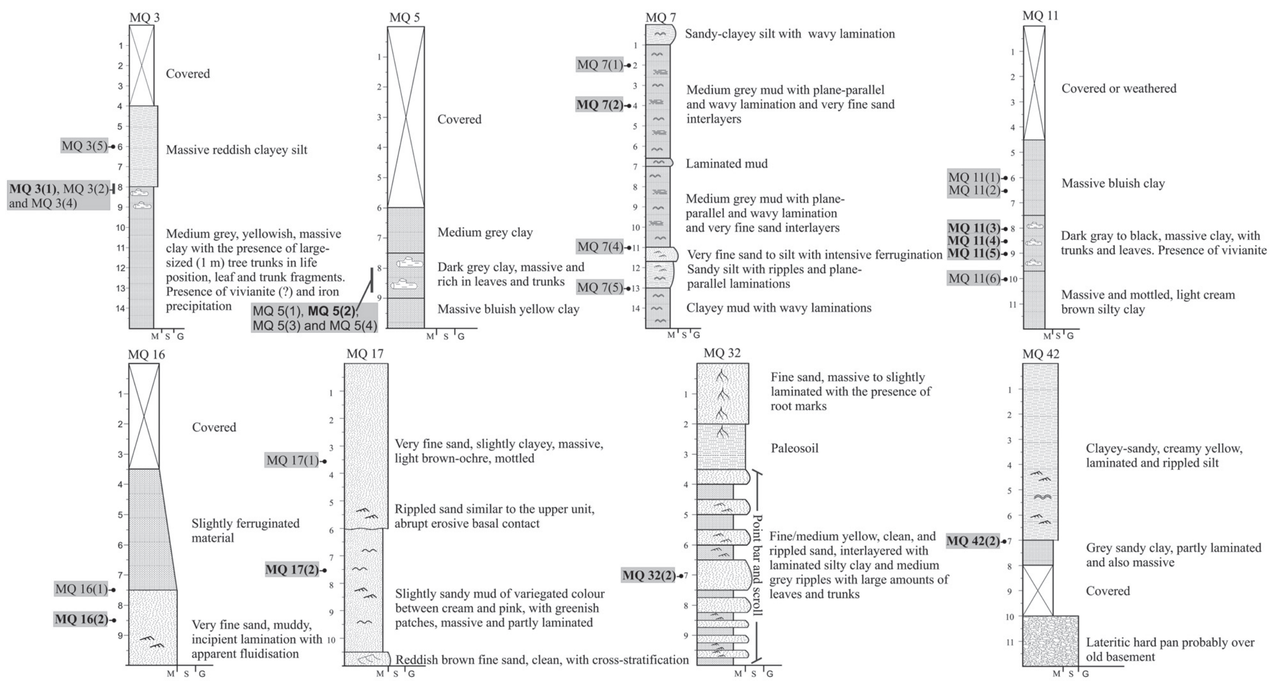

Figure 4: Profiles of the locations including samples containing pollen.

to be 667–686 cal ka BP; however, this sample was not processed for palynological analysis. Euphorbiaceae type-1 pollen was the dominant type in the MQ 32(2) sample, and Moraceae appeared as accessory pollen. The pollen assemblage found in MQ 32(2) suggested the presence of a late succession varzea forest.

Location MQ 3 showed three lithostratigraphic units (Fig. 4). Five samples were processed from this location: MQ 3(1), MQ 3(2), MQ 3(3), MQ 3(4) and MQ 3(5). Pollen was only found in MQ 3(1), which was collected from the top of a unit consisting of a medium gray, yellow, massive clay with large-sized (1 m) trunks in life position, leaves, and trunk fragments. We also found iron precipitates and the possible presence of vivianite. *Sapium* appeared as accessory pollen in MQ 3(1), and no dominant pollen was found. The pollen record could be interpreted as a late succession varzea forest; in addition, MQ 3(1) had an estimated age of 2,131–2,085 cal ka BP.

Regarding location MQ 11, samples MQ 11(1), MQ 11(2), MQ 11(3), MQ 11(4), MQ 11(5), and MQ 11(6) were processed. Pollen was found in samples MQ 11(3), MQ 11(4), and MQ 11(5), which were collected from a unit with dark gray to black massive clay with trunks and leaves, with traces of vivianite (Fig. 4). MQ 11(3) had an approximate age of 536–527 cal ka BP and included grains of Cyperaceae and Moraceae as accessory pollen and no obvious dominant pollen type. In MQ 11(4), Cyperaceae pollen type was the dominant pollen, and no accessory pollen type was found. *Alchornea* and Cyperaceae were the accessory pollen types present in MQ 11(5), which showed no dominant pollen type. The pollen assemblage described from samples MQ 11(3), MQ 11(4), and MQ 11(5) suggested the presence of a lacustrine varzea forest or a chavascal type of vegetation.

Location MQ 17 occurred in a recent morphostratigraphic unit possibly from the Holocene. This location showed three lithostratigraphic units (Fig. 4). Only one sample, MQ 17(2), was processed, collected from a unit that exhibited gray, laminated, muddy sand with undulations and fluidisation feature sand, possibly trough-cross bedded. Melastomataceae pollen appeared as accessory pollen, and no dominant pollen was found. The pollen assemblage found in this sample suggested the presence of a secondary varzea forest on this location.

All late succession varzea forest samples showed different Shannon-Weiner diversity index values (Fig. 3), with MQ 16(2) and MQ 32(2) exhibiting the smallest values from all the samples (Fig. 3). MQ 17 (2) had a value of H = 2.64, which was the greatest value found. All primary succession varzea forest samples also showed different values (Fig. 3).

Discussion

The pollen record described from the Madeira River based on the samples described here showed a forest mosaic with different varzea forest types. According to Wittmann *et al.* (2010), this type of mosaic in flooded forests originates as a result of erosion and deposition processes opening new areas for colonization in these environments.

Swamp vegetation, including chavascal and lacustrine varzea forest, is difficult to differentiate based on the pollen record, because different pollen types commonly occur in similar frequencies, as it is the case of Araceae, Cyperaceae and Poaceae (Absy *et al.* 2014). In addition, in the current vegetation, herbaceous beyond that are very abundant, the characteristic species of both environments are mainly Polygonaceae of the *Symmeria* genus and Myrtaceae of the genera *Eugenia* and *Calyptranthes* (Wittmann *et al.* 2004; Wittmann *et al.* 2010). MQ 7(2) and MQ 42(1) showed the assemblage typical of a primary succession varzea forest and they were both similar to samples taken from chavascal and lacustrine varzea forest. This similarity could be explained by the frequent occurrence of the families Cyperaceae, Poaceae and Polygonaceae in chavascal, lacustrine varzea forest and primary succession varzea forest (Junk & Piedade 1997). Another problem, the genus *Alchornea* occurs in three forest types. One possible criterion for differentiating these vegetations that would species *Alchornea discolor* occurs in varzea forest of lake and chavascal, while *Alchornea castaneifolia* occurs in primary succession varzea forest (Wittmann *et al.* 2010). However, it was not possible to differentiate the pollen of these species, raising the need for additional criteria. Swamps and lakes have high concentrations of Cyperaceae (Absy *et al.* 2014), among other types of pollen, whereas primary stages of varzea forest are characterized by high frequencies of Poaceae pollen (Wittmann *et al.* 2010). This could be used to differentiate between lacustrine varzea forest and primary succession varzea forest. Cluster analysis showed these differences by placing those samples belonging to lacustrine varzea forest or chavascal into a different group than those belonging to primary succession varzea forests, although these two groups were clustered together (Fig. 2).

The beginning of the stratification process typical of late secondary succession forests could be observed in sample MQ 17(2), as a result of the presence of Moraceae, *Pithecellobium,* and *Sapium* in the upper stratum and *Alchornea*, Melastomataceae, and Solanaceae in the lower stratum. In addition, MQ 17(2) also showed the highest Shannon-Weiner diversity index typical of communities in intermediate succession stages (Connell 1978).

Environmental diversity and plant species richness and diversity in varzea forests are known to correlate with the height and duration of flooding periods, age of plant communities, dominant channel patterns, morphodynamics, and complexity of the environmental mosaic of the floodplain (Wittmann *et al.* 2004; Latrubesse 2012). Late succession forests often present shortest height and duration of floods of all lowland varzea forests, they are also older (Wittmann *et al.* 2010); therefore, they show the highest levels of species richness and diversity. Thus, samples belonging to late succession varzea forests were quite different from each other, which cluster analysis showed by separating the different groups at different heights.

Previous research has also shown that a small number of species, even a single species, tend to dominate the vegetation in large tropical forest areas (Hart *et al.* 1989). Approximately 227 hyperdominant species are currently known from the Amazon, and 26 of them are native to the varzea forest (Steege *et al.* 2013). Therefore, species may occur at different ratios even compared to late successional stages, due to the occurrence of different dominant species.

Samples MQ 16(2) and MQ 32(2) showed the smallest Shannon-Weiner diversity indices. The lithostratigraphic unit from which MQ 16(2) was collected showed the characteristics of a channel. Thus, the pollen grains found in the sample are possibly a result of river transport, also explaining the low diversity values found here. Similarly, MQ 32(2) was collected from a point bar and scroll bar sequence, indicating that these pollen grains could have also been transported to this location.

Previous palynological analyses have shown that changes in savannah and forest vegetation occurred in the southern Amazon areas during the last glacial period (Absy & Hammen 1976; Hammen & Absy 1994; Mayle *et al.* 2000; Burbridge *et al.* 2004). Furthermore, the geological record of fluvial sediments indicates the occurrence of a strongly seasonal climate; however, high levels of sedimentation in the fluvial strip, with high water flow during floods during the Middle Pleniglacial and the initial period of the Last Glacial Maximum (LGM), and drier conditions might have occurred for much of the LGM (Latrubesse 2003). In addition, abundant fossil vertebrate fauna has been found from the Lujanense Mammal Age (Ranzy 2000; Nascimento 2008). The presence of varzea forest in LGM sediments in the Madeira River does not contradict the results found in previous studies. Research focused on the main tributaries of the Madeira River (Guaporé, Mamoré, Beni, and Madre de Diós rivers) show that they intersect at savannah areas (Ribera *et al.* 1994). Also, studies in potential areas of Bolivian vegetation (Navarro & Ferreira 2004) show that *Alchornea*, *Cecropia*, Moraceae, *Inga,* and *Sapium*, which are found in the Madeira River, are also present in its tributaries, even in those located in savannah areas. These results suggest that a varzea forest surrounded by savannah vegetation in this region during the LGM is a possibility.

Pollen grains of *Alnus, Podocarpus, Hedyosmum,* and *Ilex* were found in samples from the late Middle Pleniglacial and early LGM (Fig. 5). These taxa have been suggested as indicators of mountain forest and humid conditions (Colinvaux *et al.* 1996; Bush *et al.* 2004; Freitas *et al.* 2013). However, *Ilex* species can be also found in varzea forests of the Amazonian lowlands (Wittmann *et al.* 2006; Wittmann *et al.* 2013), and certain *Podocarpus* species can occur in gallery forests of tree savannahs in central Brazil and in other types of savannah vegetation bordering the Amazon and Peruvian plains (Ledru *et al.* 2007). The pollen from these species often relies on anemophilous transport for dispersal (Behling *et al.* 2002; Freitas & Carvalho 2012; Freitas *et al.* 2013), and there are records of *Hedyosmum* specimens collected near the town of Humaita, close to our study area (Chamberlain *et al.* 2014). Furthermore, all these species can easily reach the Amazonian lowlands, especially by river transport (Hammen & Hooghiemstra 2000). Thus, is possible that these pollen types have been transported to the current location; however, an alternative explanation could involve a process wherein these taxa could have used the varzea to advance toward Amazon lowlands during LGM.

With the advance of the savannah in the southern Amazon during the last glacial period (Absy & Hammen 1976; Hammen & Absy 1994; Mayle *et al.* 2000; Burbridge *et al.* 2004), the varzea forest may have served as a refuge for species typical from non-flooded land. Reduced rainfall during the last glacial period (Hammen & Absy 1994; Hooghiemstra & Hammen 1998; Hammen & Hooghiemstra 2000) possibly shortened the flood pulse period, producing shortened, albeit pronounced, flood period. These conditions, together with the decrease of the average annual flows, may have allowed certain dry land species to survive in the varzea forest, which may have served as a refuge for such species.

Conclusion

The paleovegetation of the Madeira River during the Late Quaternary was represented in the pollen record as a forest mosaic Our data showed the occurrence of primary succession varzea forest and lacustrine varzea forest or chavascal. These habitats showed some level of similarity; however, they may be differentiated based on the different frequencies of Cyperaceae and Poaceae pollen. Our results also show that those samples belonging to late succession varzea forests were different from each other, although those differences may be explained by the higher species richness and diversity typical from this type of forest, in addition to the existence of dominant species in the tropical forests.

Palynological and sedimentological studies conducted in the Madeira River region must be extended our understand-

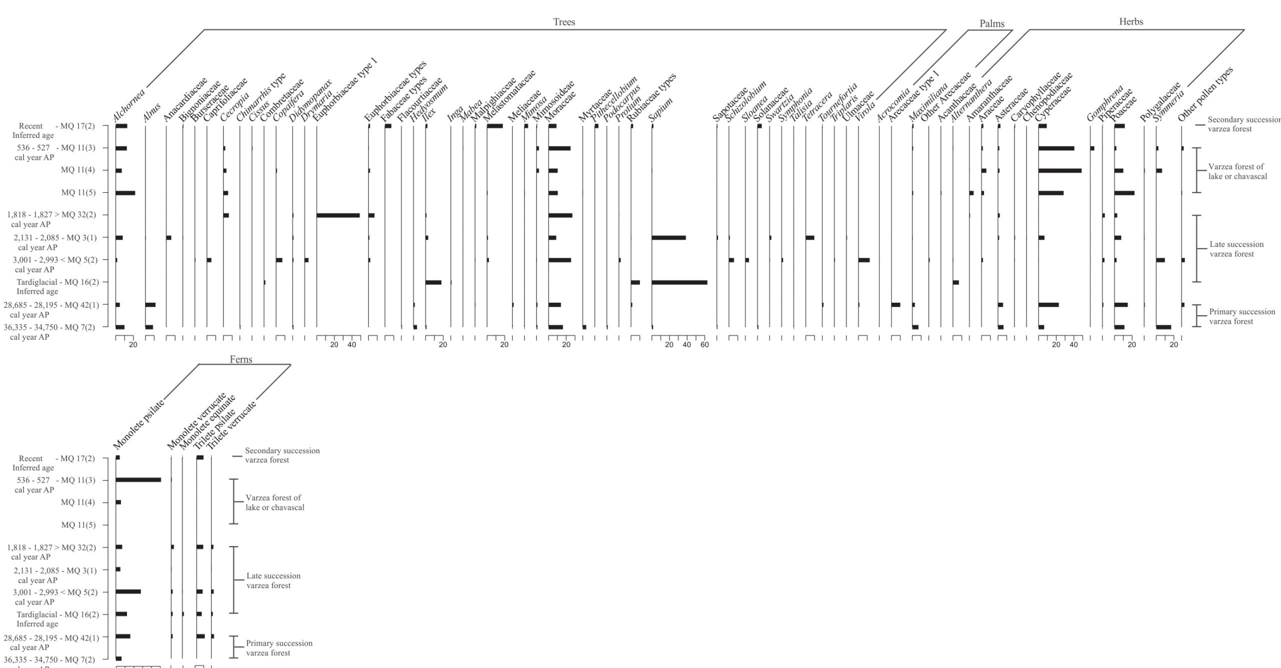

Figure 5: Percentage pollen diagrams of selected taxa from the central part of the Madeira River, Brazil.

ing on how climate and environmental changes during the Late Quaternary in Amazonian varzea forests affected the vegetation of these areas.

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