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The movement of pre-adapted cool taxa in north-central Amazonia during the last glacial

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ABSTRACT

The effects of climate change on the lowland vegetation of Amazonia during the last glacial cycle are partially known for the middle and late Pleniglacial intervals (late MIS 3, 59–24 ka and MIS 2, 24–11 ka), but are still unclear for older stages of the last glacial and during the last interglacial. It is known that a more seasonal dry-wet climate caused marginal forest retraction and together with cooling rearranged forest composition to some extent. This is observed in pollen records across Amazonia depicting presence of taxa at glacial times in localities where they do not live presently. The understanding of taxa migration is hindered by the lack of continuous interglacial-glacial lowland records. We present new data from a known locality in NW Amazonia (Six Lakes Hill), showing a vegetation record that probably started during MIS 5 (130–71 ka) and lasted until the onset of the Holocene. The vegetation record unravels a novel pattern in tree taxa migration: (1) from the beginning of this cycle *Podocarpus* and *Myrsine* are recorded and (2) only later do *Hedyosmum* and *Alnus* appear. The latter group is largely restricted to montane biomes or more distant locations outside Amazonia, whereas the first is found in lowlands close to the study site on sandy soils. These findings imply that *Podocarpus* and *Myrsine* responded to environmental changes equally and this reflects their concomitant niche use in NW Amazonia. Temperature drop is not discarded as a trigger of internal forest composition change, but its effects are clearer later in the Pleniglacial rather than the Early Glacial. Therefore early climatic/environmental changes had a first order effect on vegetation that invoke alternative explanations. We claim last glacial climate-induced modifications on forest composition favoured the expansion of geomorphologic-soil related processes that initiated forest rearrangement.

1. Introduction

The presence of plants from higher altitudinal ranges in lowland late Pleistocene pollen records has been interpreted as cooling over Amazonia (Colinvaux et al., 1996; Ledru et al., 2001). Genera like *Podocarpus*, *Hedyosmum*, *Myrsine*, *Alnus* and *Weinmannia* are found in Andean and Guyana highland sites where cooler conditions prevail. Their use as ecological indicators in fossil records is interesting not only because of their present day distribution, but also because their pollen morphology, except *Weinmannia*, is quite characteristic and hence virtually eliminates misidentifications. There has been, nevertheless, criticism to the use of such taxa as direct indicators of montane environments essentially because of two facts. First, *Podocarpus* and *Hedyosmum* are as well found in lowland biomes outside Amazonia, for example in the seasonal central Brazilian cerrados (Van der Hammen and Hooghiemstra, 2000; Ledru et al., 2007). Although montane and cerrado biomes potentially indicate lower temperatures when compared to lowland Amazonia, overall environmental conditions could vary substantially. For instance, montane species in the Andes can inhabit humid cloud forests, whereas cerrado and other savannah like habitats vary from dry, seasonally dry to locally wet (riparian) forests. The second fact is that *Podocarpus,* arguably the most used of the cited taxa, not only occurs in a wide altitudinal (and climatic) range, from sea level to high Andes, but also has edaphic constraints

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that are as large as the climatic ones. A number of *Podocarpus* species in different regions of the Neotropics are found on infertile soils at variable elevations (130–~3500 m) and climate, but not in neighbouring forests of opposite edaphic conditions (Dalling et al., 2011). That includes Amazonian lowlands where *Podocarpus* is found on white sand soils (Gentry, 1993; Van der Hammen and Hooghiemstra, 2000; Dalling et al., 2011). Therefore, in cases where there is evidence for edaphic changes, temperature solely cannot be accounted for *Podocarpus* presence outside its extant range. Additionally, *Podocarpus* emerges from lineages that arose in warm climates of the Tertiary (Quiroga et al., 2016), thus its presence in tropical lowlands can be a persistent feature since much deeper geological time than solely more recent invasions. In western Amazonia, for instance, *Podocarpus* has been recorded since at least the early Miocene (Salamanca et al., 2016) under considerably warmer conditions.

In the present paper we discuss the behaviour of the aforementioned taxa in a well-known Pleistocene pollen site, Lake Pata in NW Brazilian Amazonia. New data is presented to extend the previously published pollen record (D'Apolito et al., 2013) to an older vegetation phase yet undescribed. The integrated record could potentially represent the first entire Glacial-interglacial vegetation cycle from a lowland site (~110–10 ka, thousand years before present). "Vegetation cycle' is used in the broad sense of vegetation types that move spatially driven by climate or environment changes (a concept historically used in European temperate forests (Wright, 1997) and altitudinal gradients of vegetation (Hooghiemstra, 1984; Torres et al., 2006).

1.1. Six Lakes Hill and the Lake Pata record

The Hill of Six Lakes is a rock outcrop 300 m a.s.l. in the upper Rio Negro basin (0°16′N and 66°41′W, Fig. 1), NW Brazilian Amazon. This structure is an intrusive carbonatite (Schobbenhaus, 1984) that has undergone chemical weathering resulting in small lakes, which are isolated from fluvial systems. The region receives around 3000 mm annual rainfall that is the only source of water running into the lakes. Climate is warm and non-seasonal and vegetation growing on the Hill and surroundings is that of dense evergreen forest, but with areas of edaphically constrained vegetation, which resembles in physiognomy and composition the forests on oligotrophic soils of the Negro basin, like white sand heath forests (Anderson, 1981; Adeney et al., 2016).

Pata is one of the lakes developed on the Hill, several cores have been retrieved for sedimentology, pollen and geochemical analyses that have revealed the local paleoclimatic history for the past ~50 ka (Colinvaux et al., 1996; Bush et al., 2004; Cordeiro et al., 2011; D'Apolito et al., 2013).

We studied "core II", which is 360 cm in length and (stratigraphically) a perfect parallel to two other cores studied by Bush et al. (2004). In a first analysis we concentrated on the upper part of the core, from 0 to 285 cm, which span into the range of the radiocarbon methods (D'Apolito et al., 2013). The record for the late Pleistocene is interpreted as reflecting drier and colder conditions: less rainfall was inferred from lowered lake levels and temperature decrease is evidenced by the occurrence of what were considered montane elements (D'Apolito et al., 2013). An even dryer period spread from ~35 ka to ~10 ka, when stronger and prolonged droughts are evidenced by reworked and oxidized sediments related to clastic inputs, decrease of organic matter and erosional phases. During the Pleistocene, although drier, climate supported forests at least during the time equivalent to Marine Isotopic Stage (MIS) 3, but with a modified - non analogue - structure (D'Apolito et al, 2013). The reconstruction of vegetation during the Last Glacial Maximum (LGM, ~23 - 19 ka) is not precise because of the poor sedimentological record as a consequence of strong droughts experienced by the lake. With the onset of the Holocene, climate improved and developed into its present hyper-humid conditions. Although all published cores have radiocarbon dates, it has not been possible to date lower stratigraphic levels because of the limited C^{14} dating range. More than half of the record is beyond this limit, which hampered previous studies on the lowermost levels of the cores. Here we expanded the results by analysing the undated part of core II.

2. Material and methods

We handpicked and processed eight new samples that were available in the lower part of the core from 285 to 360 cm and analysed their pollen content. Sample processing followed standard methods (Faegri and Iversen, 1989) that consist in (1) dissolution of sediments in a 10% KOH aqueous solution, (2) acetolysis (Erdtman, 1960) and (3) heavy liquid separation by bromoform. The residues were mounted in glycerin gelatin. In each sample, we aimed to count 300 pollen grains with parallel counting of other palynomorphs (pteridophyte spores, algae and fungal spores and hyphae). Pollen was identified using mainly the pollen collection of the Palynology Laboratory of INPA and aided by pollen illustrations and descriptions published by Absy (1975, 1979), Hooghiemstra (1984), Roubik and Moreno (1991) and Colinvaux et al. (1999). A Detrended Correspondence Analysis (DCA) was performed using the 'vegan' package (Oksanen et al., 2016) for R. The DCA was performed with a square-rooted data matrix, excluding singletons in order to minimize noise. The CONISS dendrogram (Grimm, 1987) is a stratigraphically constrained cluster using sum of squares of the pollen data matrix, excluding singletons, and was done with R package Rioja (Juggins, 2015).

Extending the record to 360 cm required reinterpretation of possible ages as the radiocarbon method is overcome at ~160 cm. This was done empirically based on observed sedimentation rates and unit contacts of the dated part of the record, as well as possible climatic significance of pollen associations.

In order to interpret the fossil occurrence of the so-called montante taxa, we have plotted their extant occurrences so as to visualize whether any distributional pattern exists and is convergent among these taxa. For the purposes of our interests in the Lake Pata's record, we then restricted the occurrences to the area surrounding the Six Lakes Hill (dashed contour in Fig. 1) and checked if any of those occurrences were on lowland as opposed to the nearby Andes and Guyana Shield highlands. We did it in a conservative manner, meaning that we only used altitudinal information when they were explicitly shown on the record, rather than relying on crossing herbaria geographical coordinates with altitude data from maps or other sources. This is because sometimes longitude-latitude data in plant vouchers are not field readings but approximations. For instance, if coordinates from a close by town are used instead of the exact collection site, a difference of very few kilometres could incur in variations at different altitudes, and thus different climate, vegetation type, etc. As with altitude, soil and vegetation information were only gathered when specified in herbarium or other published records.

Because relief is an important variable for our analysis we created a SRTM DEM (90 m resolution, USGS Earth Explorer) which was mosaicked and extracted in ArcGIS and then a colour palette was applied in Global Mapper. The area covers ~1,349,571 km^2, which extends on Brazil, Guiana, French Guiana, Suriname and Venezuela. Hypsometry was analysed by resampling to 1 km using bilinear interpolation, and then the area plotted as a function of elevation.