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Amazonian paleoecological histories: one hill, three watersheds

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Abstract

Data from the Hill of Six Lakes, in the northwestern Brazilian Amazon region, provide three records of paleoclimatic and vegetation change in lowland Amazonia that span the last 170,000 years. Three lakes, Verde, Pata and Dragão, which occupy separate watersheds on the hill, provide the most detailed image yet obtained of ice-age conditions in lowland Amazonia. Well-dated sedimentary records for fossil palynological, charcoal, cation, and pigment, data are presented.

The data indicate the continuous presence of mesic forest throughout the last ice age. Oscillations of lake level are recorded and the lowstands are attributed to reduced precipitation inputs to systems delicately balanced between water loss (leakage through the floor of the basin) and gain (precipitation). Gross stratigraphy, algal remains, and paleochemistry suggest that the stands of high and low lake level were cyclic, apparently correlating precessional orbital variation. Times of lake lowstand coincide with wet season (December–January–February, DJF) insolation minima. The strongest of eight lowstand cycles occurred ca. 35,000 to 27,000 cal BP.

Even during lowstand episodes, pollen is well preserved and provides a clear signal of uninterrupted forest cover. The principal lowland elements are continuously present in the record, suggesting the long-term (Quaternary) availability of the lowland forest biome in this region. However, during the late Pleistocene the forest changed in composition with the expansion or invasion of montane floral elements creating communities of the mesic forest biome without modern analogs. While precipitation cycles were causing lake levels to rise and fall, the principal influence on vegetation appears to have been cooling. In the late Pleistocene, the population expansion of montane elements at lower elevations is consistent with a cooling of 4–5 °C. © 2004 Elsevier B.V. All rights reserved.

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1. Introduction

Climate change within the past 100,000 years is often offered as a causal mechanism underlying the modern biodiversity and biogeography of Amazonia (e.g. Bush and Colinvaux 1994; Colinvaux, 1987; Colinvaux, 1998; Cowling et al., 2001; Gentry, 1989; Haffer, 1969; Hooghiemstra and van der Hammen, 1998; van der Hammen, 1974). The principal climatic factors that may have driven changes in vegetation are temperature, precipitation, seasonality, and CO₂ concentration. As interest in the influence of changes in seasonality and atmospheric CO₂ concentrations are relative newcomers to the debate, most competing hypotheses have been expressed in terms of temperature and precipitation.

An Amazonian cooling of ca. 5 °C at the last glacial maximum (LGM) is broadly accepted among terrestrial paleoecologists (e.g. Bush et al., 2002). However, debate continues over whether the lowland neotropics were cold and dry, or cold and wet (e.g. Colinvaux et al., 2000; Colinvaux et al., 2001; Irion, 1982; Irion, 1984; Räsänen et al., 1987; Salo, 1987) during the late Pleistocene. The paucity of paleoprecipitation data has fostered different views of precipitation at the LGM. Estimates range from virtually unchanged rainfall (Colinvaux, 1998), through a reduction of about 20% (Bush, 1994), to a reduction of 45% to 55% (van der Hammen and Absy, 1994; van der Hammen and Hooghiemstra, 2000). Lying close to the uplands of the Pico da Neblina, the Hill of Six Lakes, Brazil, is ideally located to provide sensitive proxy records of past climatic change in northwestern Amazonia.

Our first long pollen history from Lake Pata demonstrated that there had not been any biome changes on the hill for at least 40,000 years, that the region was continuously occupied by closed forest, but that changes in forest composition at the LGM suggested that modest cooling was the dominant climatic change in glacial times (Colinvaux et al., 1996). We now report results of our comparative study of the histories of three lakes in the Amazonian forest at the Hill of Six Lakes that lie within separate, but proximate watersheds. We hypothesize that lake level responded primarily to changes in wet season precipitation, whereas forest cover, which would have been most strongly influenced by changes in dry season precipitation was never broken. We also demonstrate that forest composition responded most strongly to a cooling during marine isotope stage (MIS) 2.

2. The site

The Hill of Six Lakes is an ironstone inselberg that rises 300 m from the Amazon plain at 0°16'N, 66°41'W (Fig. 1). The regional climate is classified as Köppen Af, hot, equatorial, and the nearest weather station lies about 20 km distant at the Missão Taboquinha in the village of São Gabriel da Cachoeira. Annual precipitation at the mission ranges between 2914 and 3652 mm per annum. Rainfall is somewhat lower in June–July–August than other months, but no marked dry season is evident. The precipitation is influenced by three factors, local convective activity, which

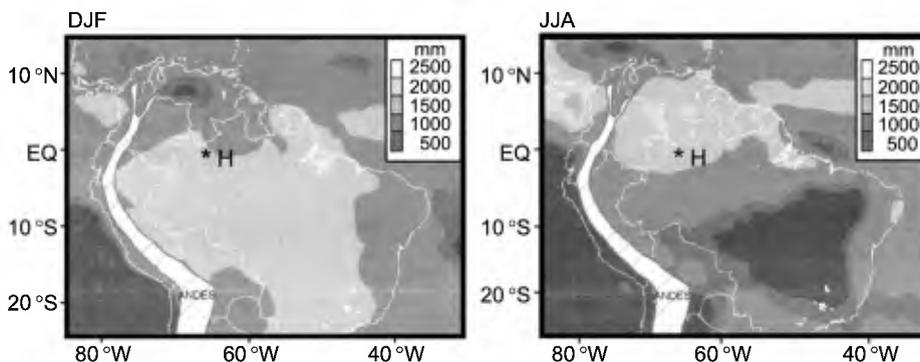


Fig. 1. Sketch map showing the relative location of the Hill of Six Lakes, Brazil, relative to JJA precipitation and DJF precipitation. Precipitation data are based on Data from Tropical Rainfall Measuring Mission (TRMM) for 1998 and 1999 (data courtesy of Z. Liu).

accounts for most of the rain events (Radambrasil, 1976) the migration of the Inter Tropical Convergence Zone (ITCZ) and moist easterly trade winds bringing moisture from the Atlantic. The average mean monthly temperature is 25 °C with a high of 30 °C and a low of 21 °C. The coolest nights are associated with “friagem” events, when fronts of cold air sweep up from Patagonia.

Radambrasil maps show the vegetation below 600 m elevation of this region as dense tropical rain forest. We observed that the forest at the base of the inselberg was composed of large trees forming a canopy 25–30 m above the ground. However, the steep sides and undulating plateau of the inselberg carried a forest of smaller stature. Thin soils supported trees that formed a canopy at 10 to 15 m, and the forest had a structure more typical of the forests found on white sand soils than true wet forest. Growing as emergents were some trees typical of true rain forest environments. These included Lauraceae, *Hevea* (Euphorbiaceae), Sapotaceae, *Licania* (Chrysobalanaceae), *Caryocar* (Caryocaraceae), and *Brosimum* (Moraceae). It should be noted that the *Caryocar* seen on the Hill of Six Lakes was a large rain forest tree, not the savanna tree *C. brasiliensis*. Other common forest taxa included *Alchornea* (Euphorbiaceae), Anacardiaceae, Annonaceae, Burseraceae, *Cordia* (Boraginaceae), *Gnetum* (Gnetaceae), Melastomataceae, Meliaceae, Myrtaceae, Rutaceae, and Simaroubaceae. *Iriartella setigera* (Arecaceae), and *Bactris* (Arecaceae) were common in the understory. In open areas *Cecropia* (Cecropiaceae), Melastomataceae, and *Clusia* (many species; Clusiaceae) formed a shrub layer. *Heterostemon ellipticus* (Orchidaceae), *Sobralia liliastrum* (Orchidaceae), Bromeliaceae, and *Selaginella* (Selaginaceae) formed a groundcover. An area that had been burned in 1983 supported early successional forest composed of *Cecropia*, *Vismia* (Clusiaceae) *Croton* (Euphorbiaceae), *Swartzia* (Caesalpinioideae), *Peltogyne* (Caesalpinioideae), *Antonia ovata* (Antoniaceae), *Licania*, Ochnaceae, Burseraceae, and Meliaceae.

During the 1991 field season we conducted limnological studies, and raised sediment cores from the plateau region of the inselberg. Cores were raised from lakes Dragão (Dragon), Pata (Duck) and Verde (Green), and a *Mauritia* (Arecaceae) swamp, Esperança (Hope). In this paper we present and analyze the data from Dragão, Pata and Verde, each of which

occupies its own watershed. Importantly, the three watersheds are quite different from one another. An appreciation of the differences between the catchments is critical to interpreting the paleoecological records.

Dragão was a steep sided basin with almost no soil overlying the rock surface. A recent fire (set by humans) had led to a local replacement of the forest with early successional species. The lake had two lobes forming a dumbbell shape about 120×50 m. One of the lobes was 13 m deep and the other 14 m deep, with the area between them about 10 m deep. A core was raised from the center of the deepest lobe. Despite being without evident inflows or outflows, we observed that the lake level dropped by 1–2 m during our 10-day stay. Clearly, there is more than evaporative loss causing changes in water-level in this lake. In 1983, during the El Niño event a geological team found this lake to be dry (Justo and Quadros, 1983). Thus this lake has unstable water levels and under extreme conditions dries out.

Pata lies in a forested watershed with cliffs along one margin, but with more gentle slopes on the other side. The broad shallow basin offered a relatively large watershed compared with Verde and Dragão, probably covering 5–10 times the surface area of the other watersheds. A marshy fringe had established in some areas and supported *Ludwigia* (Onagraceae), *Mauritiella* (Arecaceae), *Euterpe* (Arecaceae) and *Mauritia*. Flood marks on the shoreline and vegetation showed that lake level had recently fallen about 50 cm and that during wetter episodes the lake was regularly 2 m deeper than when we visited it. An adjacent *Mauritia* swamp, Esperança, was separated by a low hump of land, and during the wet season the swamp may be continuous with the main body of Pata. Lake Pata is about 300 m in length with a flat-bottomed main basin that is 3 m deep, and three smaller sub-basins on the northern side of the lake. Two of these basins were ~2 m deep, but the third was 27 m deep. A core was raised from the center of the main (3 m deep) basin. Both light and dissolved oxygen concentration declined close to zero at 3 m depth.

Verde was a strikingly green lake in marked contrast to the brown water of the other two systems. The basin that Verde occupied had sheer sides that formed cliffs 2–30 m high around the lake. A 1 m

change in recent lake level was noted based on the surrounding vegetation. Struck by the small size of the lake's watershed, we made a field estimate that this lake drained an area that was approximately 450×150 m, while the open water was about 400×100 m. The lake was oval with a slight embayment at the northern end. The lake bed sloped from 7 m depth at the southern end down to 10.5 m depth close to the northern end. The northern embayment lay beneath a 30-m-high cliff and had a water depth of 22 m. A core was raised from the center of the main lake basin from a depth of 10 m.

Thus the three watersheds differed in that Dragão and Verde were both small and steep sided, whereas Pata was large with an extensive seasonal backswamp. Dragão had an unstable water level, whereas the other lakes appeared to be relatively constant, i.e. may fluctuate by a meter or two, but do not dry out.

3. Methods

Samples of moss were collected from fallen trunks at five locations to provide modern pollen spectra. Each sample was collected from about a 20 m² area. Due to the dry nature of the microclimate on the inselberg, moss development was limited to relatively small clumps.

Cores were raised from a rubber raft using a Colinvaux–Vohnout piston corer (Colinvaux et al., 1999) in October of 1991. We avoided coring the deep holes in Verde and Pata as they were so steep sided that we suspected slumping of side-wall material would be a significant problem in obtaining a meaningful record. Cores were raised from the broad flat, bottom of each lake in 1 m sections. Parallel cores were collected at each coring station. After completing the first core sequence, we shifted the coring platform laterally by about 0.5 m and then started the parallel core 0.5 m above the mud–water interface. Consequently, the parallel core was vertically offset by 0.5 m to ensure that any material dropping from the bottom of a core during recovery was represented in the other core. Cores were returned unopened to the laboratories of the Smithsonian Tropical Research Institute, Panama, where they were opened, described and subsampled for pollen, paleochemistry and ¹⁴C analyses.

Sediment subsamples (0.5 cm³) were taken for pollen analysis, the spacing of sampling varied between the cores. Dragão was subsampled at 10 cm intervals, Verde was sampled at 5 cm intervals and Pata was sampled at 5 cm intervals with sampling at 2 cm intervals within the core section representing the glacial maximum. Pollen samples were prepared using standard methods, *Lycopodium clavatum* spike (Stockmarr, 1971) 10% KOH, Acetolysis, HF, mounting in glycerol (Faegri and Iversen, 1989). Pollen counts were made on Leitz Ortholux II photomicroscopes at x 400 and x1000. 300 pollen grains were counted in almost all samples and photographs of most of the taxa have been published (Colinvaux et al., 1999). Palynomorph diversity is a minimum estimate, as many plant taxa could be included within a single palynomorph, e.g. Melastomataceae. Unless otherwise noted, diversity is expressed as the number of palynomorphs identified per 300 pollen grains counted.

The sedimentary pigments were extracted in darkness for 48 h with 20 ml of 90% acetone and 5% diethyl aniline (Wetzel and Likens, 2000). The absorbance of chlorophyll degradation products was measured as the peak height above envelope, using a recording double beam spectrophotometer (1 cm cell), usually at 663–665 nm. Sedimentary pigment degradation units (SPDU) are reported as absorbance/1 cm path in 100 ml of acetone per g organic weight of sediment.

Subsamples (1 cm³) were taken for the determination of cation and heavy metal concentrations. Following extraction in 20 ml of 1 M acetic acid and 25% (v/v) hydroxylamine hydrochloride (heated gently), 5 ml of the supernatant were read in a flame spectrophotometer to determine the concentration of heavy metals and cations bound to exchangeable oxides and carbonates. The residue was oxidized by heating to 65 °C with 10 ml 30% hydrogen peroxide (Chester and Hughes, 1967). A 5 ml aliquot of the supernatant from this digest was read in the flame spectrophotometer to determine cations and heavy metal concentrations bound to organic matter. In both cases cations and heavy metals (Ca, Mg, K, Na, Al, Fe, Mn, Cu) were measured by atomic spectrophotometry (IL 353) using a 2-cm-long solids burner with an air–acetylene or air–nitrous oxide flame. Two further aliquots, 10 ml from each digest supernatant,

were diluted to 25 ml with distilled water, and phosphate was determined with a phosphomolybdate/ascorbate reagent (Wetzel and Likens, 2000). Although calculated separately the exchangeable and organic concentrations were combined to provide total weight of all cations and heavy metals, and expressed as percent dry weight. A full suite of chemical analyses was run on Verde, analyses on Pata were restricted to loss-on-ignition (LOI), SPDU, Ca²⁺, Na⁺ and K⁺. Dragão was analyzed for LOI only.

The first dates obtained on Pata were bulk dates on traditional ¹⁴C assays. As accelerator mass spectroscopy (AMS) dating became more widely accessible we re-dated the cores, wherever possible using hand-picked organic remains.

Pollen diagrams were plotted in TILIAGRAPH (Grimm, 1992), and statistical analyses were carried out in PC-ORD4 (McCune and Mefford, 1999). PC-ORD4 includes a corrected version of detrended correspondence analysis (DCA; Hill, 1979) that overcomes the sequence sensitivity identified by Oksanen and Minchin (1997).

3.1. Nomenclature and pollen taxonomy

We follow the nomenclature of Cronquist (1988) for our base taxonomy. Ecological notes are based on extensive examination of the herbarium sheets in the Chicago Field Museum of Natural History, the New York Botanical Gardens, and the Missouri Botanical Gardens, plus our own field observations.

The pollen and spores of the three lakes, Dragão, Pata and Verde were counted by Moreno, De Oliveira, and Bush, respectively. Verde was the first lake counted and the pollen taxonomy of this record is consistent with, but a little less refined than, counts made later by Moreno and De Oliveira. The difference being that De Oliveira and Moreno mounted an extensive effort to increase the modern pollen reference collection for this region. More than 400 palynomorphs were described in these sediments and these are attributed to >320 taxa. In order to render the data comparable for statistical purposes, we adopted the pollen taxonomy used in the Verde record which still provides 197 pollen types.

Unknown pollen types are a feature of all lowland neotropical records. It is our practical experience that pollen of species favored by disturbance, e.g. *Cecro-*

pia and Araliaceae, are relatively easy to identify. Similarly, the montane elements, e.g. *Podocarpus*, *Alnus*, *Myrsine* (ex *Rapanea*) and *Drimys* are readily identifiable, as are weedy species of open ground, e.g. *Borreria*, *Cuphea* and Poaceae. However, elements of mature lowland forests, both trees and lianas, provide a host of pollen that we cannot yet identify. Many of these taxa produce small tricolporate pollen types that are difficult to separate reliably into types, let alone identify. As a rule of thumb, it is our experience that “unknown” tricolporate pollen taxa in these records are derived from trees and shrubs. Accordingly, we include the unidentified tricolporate pollen within our arboreal pollen sum. Any error that we induce through this is certainly smaller than omitting this group from the arboreal sum.

4. Results

4.1. Stratigraphy

The cores raised from Dragão, Pata and Verde are all composed of similar sediments. The upper sections of the cores are comprised of gyttja derived from local ironstone and organic detritus. The color of this material ranges from khaki, to orange–brown as it dries. The oldest core sections at Verde and Pata are characterized by a black, highly compacted amorphous gyttja (Table 1: Fig. 2). All of these deposits are consistent with being deposited very slowly in a closed-basin system.

The stratigraphies of the Dragão and Pata records were precisely replicated in the parallel cores. As the first meter of core was raised from Pata, the lower 23 cm of sediment dropped out of the core barrel. A distinct form of gyttja was evident in the cores, in which the mud appeared to be drier and showing a tendency to forming small clumps, hereafter described as nodular gyttja. Consequently the transition from the yellow nodular clays to the black gyttja at 83 cm was lost. However, in the parallel core (vertically offset by 50 cm) the transition into and out of the nodular yellow clays was present in its entirety.

We are confident that due to the well-defined stratigraphic markers in cores from Pata and Dragão, dates on the respective primary and parallel cores can be combined to create the chronology of each lake.

Table 1
Stratigraphy of cores from Dragão, Pata, and Verde, Hill of Six Lakes, Brazil

Dragão	
0–50 cm	Yellowish nodular gyttja
51–60 cm	Khaki nodular gyttja
90–61 cm	Khaki gyttja
Pata	
0–60 cm	Soft green–black gyttja
60–63 cm	Transition between green black gyttja and nodular yellowish gyttja
63–83 cm	Yellowish nodular yellow gyttja
83–166 cm	Bluish black gyttja
200–212 cm	Organic silty clay with a sharp lower boundary sharp boundary
212–289 cm	Light brown silty clay
300–305 cm	Light brown silty clay
305–311 cm	Dark brown silty clay
311–323 cm	Light brown silty clay, very distinct layer
323–336 cm	Dark brown silty clay
336–347 cm	Light brown nodular clay (hard but breaks after pressure)
347–355 cm	Gray nodular clay
355–361 cm	Red (oxidized) sticky clay
361–388 cm	Dark gray very nodular clay
400–425 cm	Gray clay (sticky)
425–442 cm	Dark gray very granular sticky clay
442–460 cm	Dark brown sticky clay
460–465 cm	Dark gray, transition to nodular clay
465–495 cm	Gray drier nodular clay
500–532 cm	Brown clay sediments
532–537 cm	Grayish clay very compact
537–542 cm	Brown soft clay
542–577 cm	Light brown soft silty clay
577–583 cm	Gray nodular clay
583–586 cm	Brown soft silty clay
586–588 cm	Gray soft silty clay
600–610 cm	Very soft clay
611–618 cm	Very sticky silty clay
618–621 cm	Dark gray nodular clay
621–626 cm	Brown soft silty clay
626–640 cm	Gray nodular clay
640–654 cm	Brown soft sticky silty clay
654–664 cm	Gray nodular clay
664–688 cm	Brown soft clay
688–691 cm	Gray soft clay
Verde	
0–25 cm	Nodular dark green/brown gyttja
25–233 cm	Smooth khaki gyttja
233–235 cm	Gray clay
235–237 cm	Red/brown gyttja
237–243 cm	Gray green clay
243–255 cm	Gray clay
255–269 cm	Smooth khaki gyttja, nodular at base

Table 1 (continued)

Verde	
269–274 cm	Gray clay
274–284 cm	Brown gyttja
307–315 cm	Smooth khaki gyttja, nodular at base
312–325 cm	Smooth khaki gyttja, nodular at base
325–334 cm	Khaki gyttja
335–337 cm	Orange brown gyttja
337–348 cm	Khaki gyttja
348–399 cm	Black consolidated gyttja
400–435 cm	Khaki consolidated gyttja
435–439 cm	Brown consolidated gyttja
439–445 cm	Gray green consolidated gyttja
445–460 cm	Gray/black consolidated (dry) gyttja

4.2. Chronology

The chronology of these lakes was established using a blend of bulk radiocarbon ^{14}C dates and AMS dates. In Dragão and Pata dates from two cores are combined to provide a workable chronology. Very clear stratigraphic markers allowed the cores to be aligned precisely. Calibrated ages <20,600 ^{14}C years are based on CALIB version 4.2 (Stuiver and Reimer, 1993), maximum and minimum values are based on 1 standard deviation. Ages 20,600–45,000 ^{14}C years were calibrated using the polynomial equation advocated by Bard (1998).

Merging the 15 dates on the two Dragão cores provides a chronology in which it is evident that there are some outliers (Fig. 3). We believe it prudent to reject three dates marked by (*) on Table 2. The rationale for rejecting these dates is that they are clearly not linear, and to accept them would mean rejecting a greater number of other dates.

These data suggest a sedimentary hiatus at 50 cm depth that represents the period from ca. 40,000 cal. BP to 20,000 calibrated years BP (all ages will be expressed as calibrated years BP; henceforth cal. BP).

In the Pata record 13 dates form the basis of the chronology; all the dates are accepted (Table 3).

Pata sediments reveal a marked reduction in the rate of accumulation between 76 and 84 cm depth. This zone equates to the period ca. 36,000 and 26,600 cal. BP. During this 10,000-year period, just 6 cm of sediment were deposited. Such a low rate of accumulation is strongly indicative of a low lake stand, or of intermittent low water. Because pollen concentrations

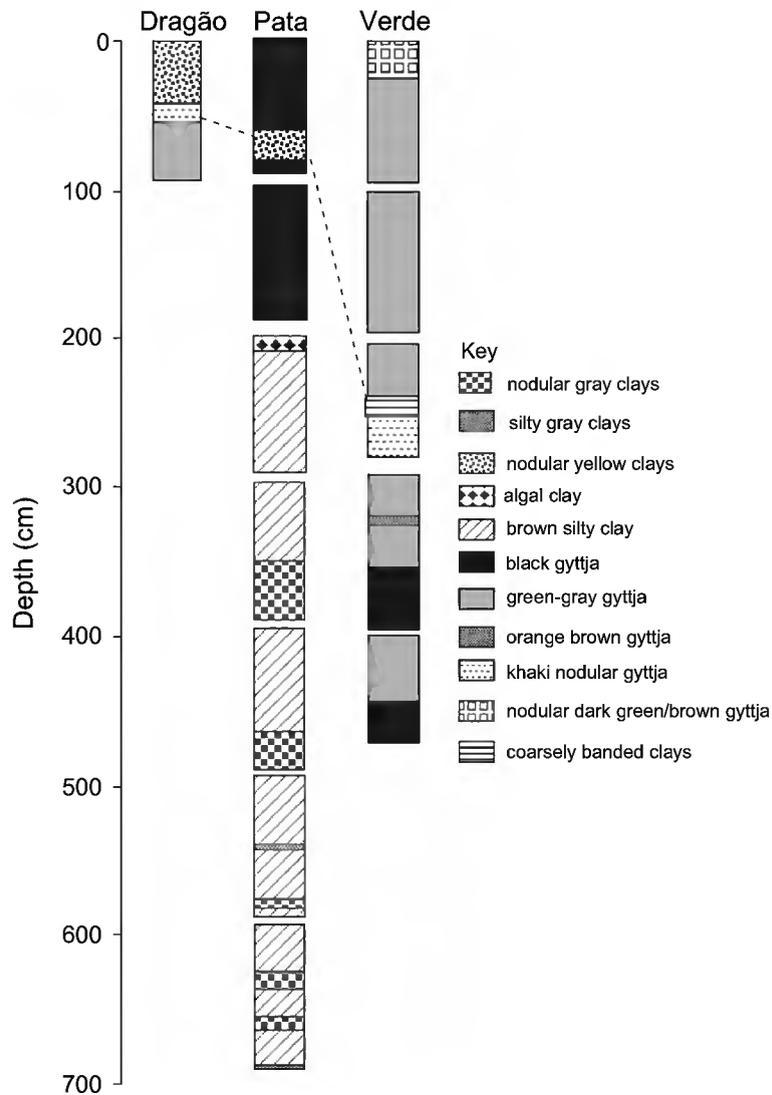


Fig. 2. Comparative stratigraphy of Lakes Dragão, Pata and Verde, Brazil.

in this zone are remarkably high we do not believe this is a simple, single, drying event.

At Verde the chronology is based on 17 AMS dates (Table 4).

The Verde dates indicate that there was no Holocene sediment collected. One date that appears to be an outlier (2920 cal. BP at 7.5 cm) is excluded from the calculation of regression lines. Sedimentation appears to have been generally slow, although faster than in the other two lakes. The chronology beyond 27,750 cal. BP is problematic. Two possible

hypotheses are that at some time prior to 50,000 cal. BP there was sediment accumulation in the basin and the presence of a deep lake, but that from at least 50,000 cal. BP until 27,750 cal. BP there was almost no net accumulation of sediment, implying a dry lake bed. The alternative is to accept the date of 41,090 cal. BP and all dates below that horizon, and then discount the four dates between 255 and 290 cm as being contaminated by old carbon during phases of oxidation of a dry lake bed. Rowe et al. (2003) argue that mobile humates can leach downward providing

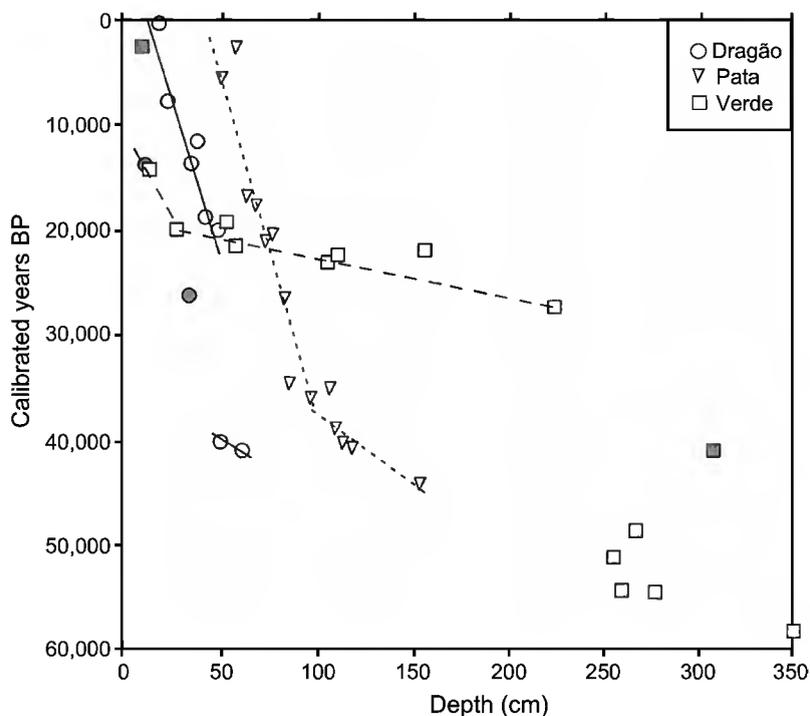


Fig. 3. Depth age curves for AMS dating of lakes Dragão, Pata, and Verde, Brazil. All ages are in calibrated years before present (cal BP). Outliers are shown as shaded symbols, accepted dates are shown as open symbols.

artificially young ages, and that macrofossil or humin fractions are more reliable. Having identified this problem, we dated one level at 255 cm using pollen and organic solids that floated at a specific gravity of 2. This sample provided a ^{14}C age of $>50,300$ BP. Tentatively, we conclude that Verde contains a sedimentary gap from ca. 27,000 BP until at least 50,000 BP. For the remainder of the core description we will adopt the chronology that rejects dates marked with an asterisk.

It should also be noted that the bottom of this basin may not have been reached. On the sixth coring drive, which started at 460 cm depth, the corer was hammered 15 cm into the sediment, but could not be extracted. The loss of the coring rig prevented collection of a parallel core.

4.3. Results of paleochemistry

The paleochemical data from Pata (Fig. 4) reveal some striking patterns and their interpretation form a framework for discussing the pollen data. Concen-

tration of SPDU in the Pata record are close to zero in most samples although a few samples show markedly higher than zero values. Although SPDU are usually taken as a proxy for lake productivity, in this instance the zero values do not indicate an absence of productivity. The observed fluctuation in SPDU concentrations is entirely consistent with the post-depositional oxidation of pigments in a system with low productivity, slow sedimentation and some free oxygen at the mud–water interface. Under the present depositional environment pigments are not preserved, and so only when the lake is deeper would there be significant concentrations of SPDU. The three cations K^+ , Na^+ and Ca^{2+} all have remarkable records, especially as they are not as closely correlated as would usually be expected (Wetzel and Likens, 2000). Ca^{2+} concentrations rose from $<50 \mu\text{g}/\text{cm}^3$ to sustained values between 200 and $300 \mu\text{g}/\text{cm}^3$ between 510 and 330 cm depth. This increase may represent a period of increased dissolution of calcium from the parent material, though it is not matched in the Na^+ and K^+ spectra. An alternate possibility is that the

Table 2
Radiocarbon dates from the principal and parallel core from Lake Dragão, Brazil

Sample	Age (¹⁴ C years BP)	Calibrated age (cal BP)	C ¹³ /C ¹² (‰)	Depth (cm)
β-94304	1780±60	1700±80	-25.9	2
Cams 41076	5370±50	6150±100		3
Cams 41079	12,290±60	14,350±380		8*
β-94305	8050±60	8910±110	-27.5	20
Cams 41077	22,630±120	26,190±450		33*
β-94306	11,960±60	13,730±170	-28.3	37
OS-5137	35,200±240	40,160±670	-35.4	49
OS-5136	34,300±590	39,560±820	-33.83	55
β-68526	37,540±680	41,400±250	-33.6	57–62
<i>Parallel core</i>				
β-94307	990±680	1080±630	-26.6	1
Cams 41078	5940±50	6770±70		5
β-94308	780±50	710±30	-26.4	13*
Cams 47772	12,240±60	14,210±310		34
Cams 47773	15,870±160	18,610±500		41
Cams 47774	18,640±80	21,860±330		48

All dates are AMS dates with the exception of β-68526 which was a bulk ¹⁴C date. An asterisk denotes a date that appears to be an outlier. Ages calibrated according to CalPal (Weninger et al., 2004). C¹²/C¹³ values shown when measured. For AMS dates a -25‰ δ¹³C is assumed.

Table 3
Radiocarbon dates from the principal and parallel core from Lake Pata, Brazil

Sample	Age (¹⁴ C years BP)	Calibrated age (cal BP)	C ¹³ /C ¹² (‰)	Depth (cm)
β-63417	5800±70	6590±80		50–55
β-75109	17,850±300	20,890±530	-29.4	72–77
β-75110	31,390±540	35,650±620		105–110
β-68529	38,860±920	41,990±490	-31.4	115–120
β-68530	42,010±1240	43,640±1000	-34.4	155–160
<i>Parallel core</i>				
βv-91489	14,230±60	17,320±170		62.5
β-90306	15,560±60	18,360±300		67.5
β-90307	18,020±70	21,140±530		73.5
β-94303	22,600±90	26,140±440	-31.1	82
β-91490	30,830±220	35,010±320		84.5
β-88941	32,010±630	36,700±1080		96.5
β-89715	34,650±420	39,820±690		106.5
β-88942	37,830±1300	41,560±540		113.5

All dates on core 1 were bulk ¹⁴C dates, whereas those on the parallel core were AMS dates. Ages calibrated according to CalPal (Weninger et al., 2004). C¹²/C¹³ values shown when measured. For AMS dates a -25‰ δ¹³C is assumed.

Table 4
Radiocarbon dates from Lake Verde, Brazil

Sample	Age (¹⁴ C years BP)	Calibrated age (cal BP)	C ¹³ /C ¹² (‰)	Depth (cm)
Cams-47775	12,050±50	13,840±150		2
Cams-47776	2790±50	2885±60		7.5*
β-95704	12,480±60	14,570±340	-29.1	12
Cams-47777	17,100±70	20,320±410		26
Cams-47778	16,410±70	19320±330		52.5
β-95705	18,430±100	21,670±260	-27.9	57
β-95706	19,740±70	23,030±200	-27.0	105
Cams-47779	19,170±120	22,430±250		110.5
Cams-47780	18,680±130	22,000±440		155
OS-1320	23,600±450	27,510±640	-27.7	223
Cams-63213	>54,100			250
Cams-100577	>50,300			255
Cams-63214	42,900±2100	44,780±1860		266*
Cams-63215	50,500±3700			274*
Cams-62776	35,600±1400	39,740±1220		307*
Cams-62777	51,900±2700			350*
OS-1321	>43,800		-35.02	448

An asterisk denotes a date that appears to be an outlier. Ages calibrated according to CalPal (Weninger et al., 2004). C¹²/C¹³ values shown when measured. For AMS dates a -25‰ δ¹³C is assumed.

increased concentrations of Ca²⁺ could represent a new source of groundwater with a different chemical signature. Concentrations of K⁺ appear to follow cycles of brief, very high peaks separated by relatively long periods of low concentrations. The record of Na⁺ concentrations shows a strong, steady decline throughout the Pleistocene, with the cyclic variation evident in the K⁺ record only weakly superimposed on this general pattern.

The Verde paleochemistry (Fig. 5) record shows some similarities with Pata. SPDU have generally low values, but again there are wildly fluctuating values. K⁺, Na⁺, and Ca²⁺ show cyclic peaks, but in this core they are clearly correlated. A peak of phosphorous concentrations between 180 and 120 cm corresponds to a time of rapid sedimentation (Fig. 3). This core segment also represents an interruption in a general decline in Fe concentration that begins at about 350 cm and continued until about 50 cm depth.

4.4. Modern pollen spectra

The modern pollen spectra proved to have low diversity with an average of 32.2 pollen taxa per sample. All five samples had unusually high percen-

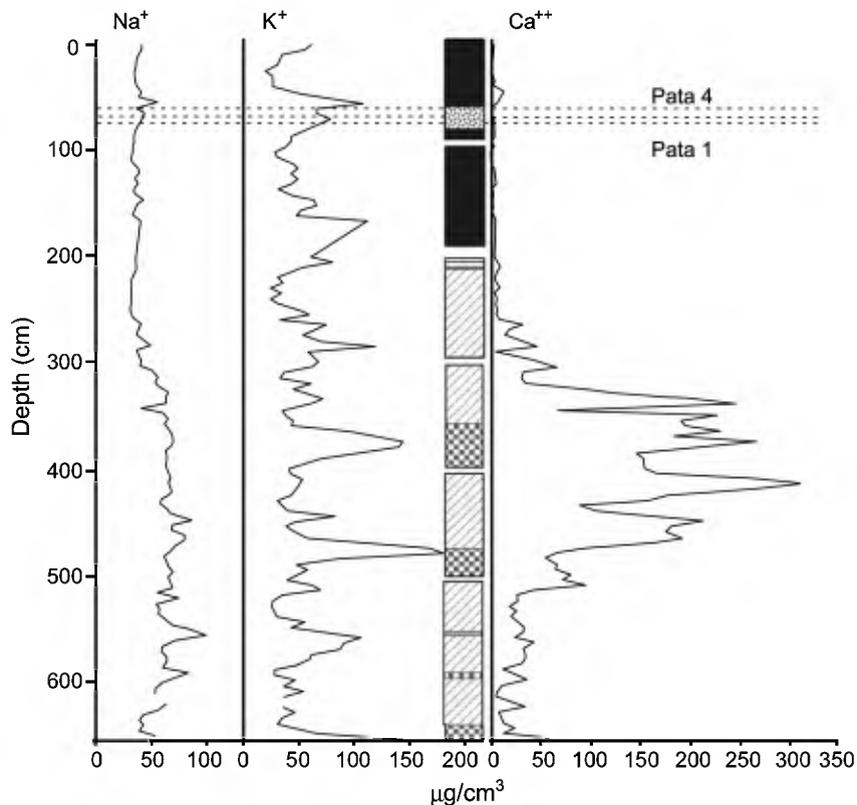


Fig. 4. Results of paleochemical analysis of sediments from Lake Pata, Brazil.

tages of *Alchornea/Aparisthemum*. It is possible that *Alchornea/Aparisthemum* are indeed the dominant contributors to pollen rain on the inselberg, but as this did not fit with our field observations of the relative commonness of these taxa, three other hypotheses should be considered. One is that the moss polsters tended to form close to these trees, and the second is that selective preservation of pollen removed most other pollen types. The third (preferred) possibility is that the moss polsters did not contain an entire year of pollen influx, but were simply holding species that were flowering while, or shortly before, we were collecting. Given these doubts we do not use the modern spectra in formal analyses, but they do provide an insight into the range of pollen types that are currently found on the inselberg (Fig. 6).

In addition to *Alchornea/Aparisthemum* many of the pollen types that were abundant in the fossil spectra are found to be abundant in the modern spectra. Myrtaceae, *Ilex*, Urticaceae/Moraceae, Mela-

stomataceae, Flacourtiaceae, Sapotaceae and Clusiaceae are abundant in most samples. Some of the rarer taxa that are informative regarding the mosaic of habitats on the inselberg are *Mauritia*, *Macrolobium*, *Pachira*, and *Polygala* from the wetlands, and *Apeiba*, *Aphelandra*, *Bombax*, *Cedrela*, *Cissampelos*, *Cynodendron*, cf. *Lecythis*, *Mabea*, *Tovomitopsis*, and *Trichilia* from the forests. A single grain of *Myrsine* (ex *Rapanea*) was found. We did not observe *Myrsine* on the Hill, but that certainly does not preclude its presence. *Myrsine* generally occurs as an element of the lower cloud forest (Gentry, 1993) and its pollen has not been found in our extensive surveys of Andean modern pollen samples outside of the plant's normal range (Weng et al., 2004).

4.5. Ordination of fossil pollen data

The percentage pollen data for the three sites were combined to form a single matrix for statistical

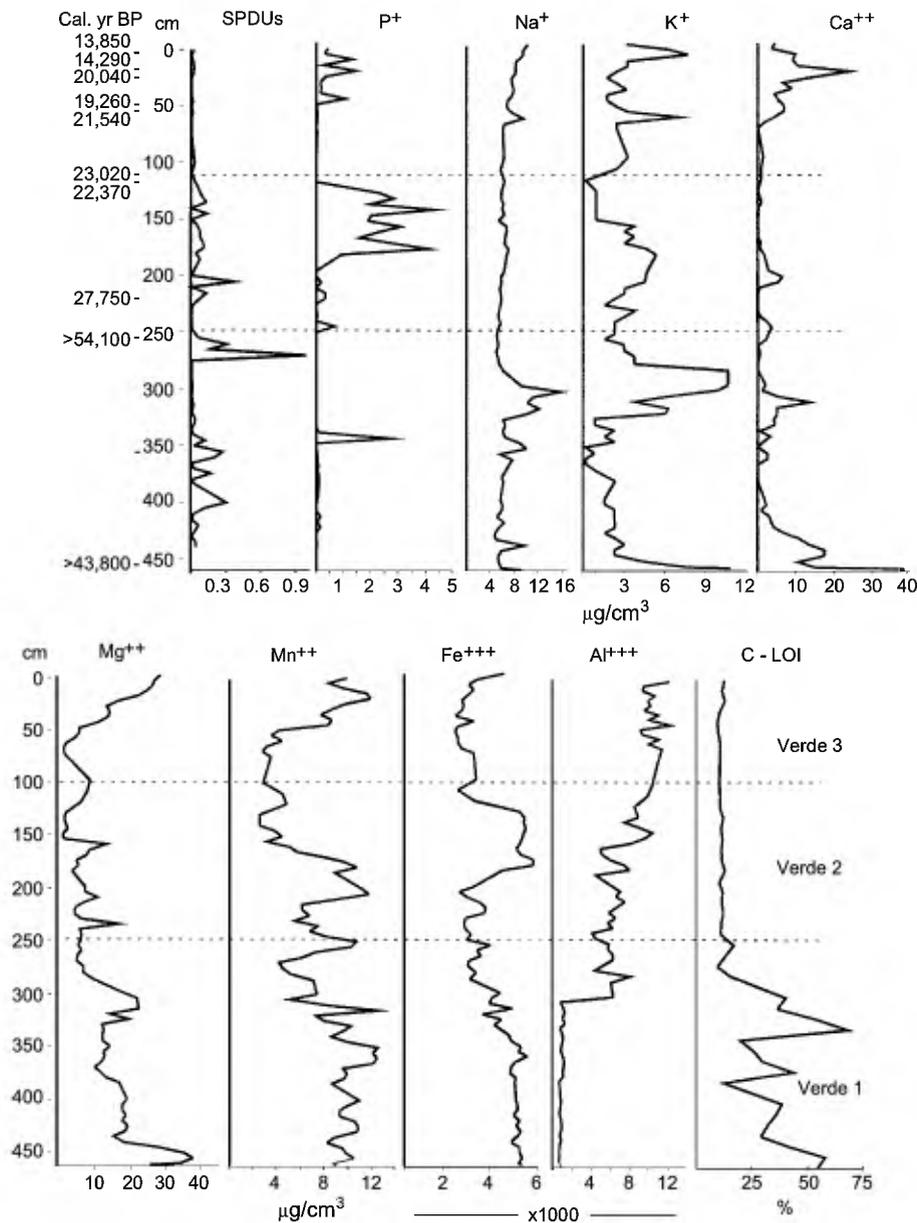


Fig. 5. Results of paleochemical analysis of sediments from Lake Verde, Brazil.

analyses. The total of >400 palynomorphs documented in the three records was reduced to 170 taxa for which there were positive identifications and concordance between the researchers. The data were log transformed to reduce exaggerating the importance of over-represented taxa (Birks, 1986) prior to ordination using DCA. This data set was so noisy (i.e.

it had so many rare taxa that occurred once or twice) that acceptable levels of variance were not reached after 400 iterations. The data set was reduced to 122 taxa by excluding all taxa that were not recorded in at least five samples. As there was a tendency for the samples of each lake to cluster, we wanted to rule out the possibility that observer bias was driving the

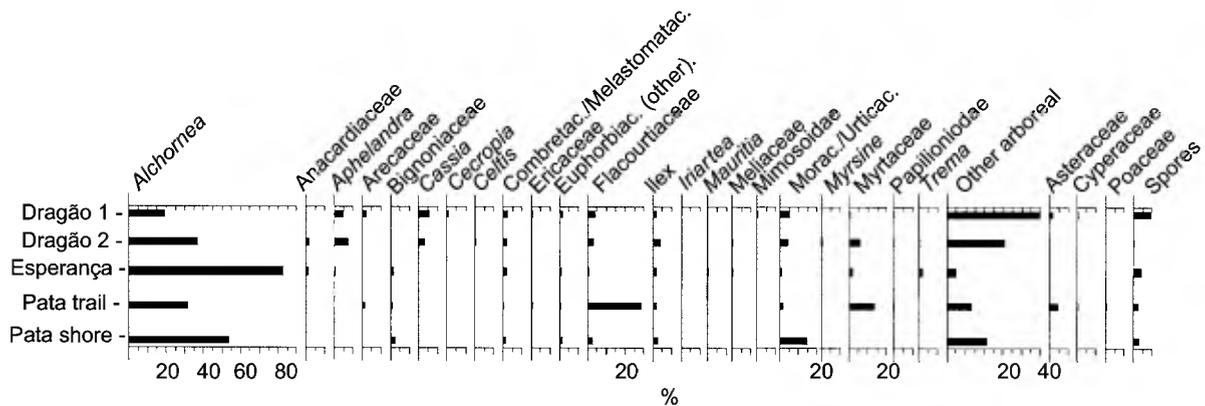


Fig. 6. Principal taxa found in modern pollen spectra obtained from moss polsters collected October 1991 near Lake Verde on the Hill of Six Lakes, Brazil.

results rather than a genuine ecological pattern. To test for this we ran the analysis again using only the 25 most readily recognizable, most common, taxa. The result of this ordination was indistinguishable from the run using 122 taxa. A similar result was obtained by Terborgh and Andresen (1998) who found that ordinations of Amazonian forest data were consistent regardless of whether the data were treated at species-level or simplified to the family level. In our analysis, as the minimal data set produced results with as much ecological information as the more complex data set, we present this simpler, taxonomically more robust, analysis.

Given the proximity of these lakes, a remarkable degree of structure is evident in the DCA results. Not only is there minimal overlap between the different lakes, but there is also a strong age-relationship evident among samples within each lake. Furthermore, it is also clear that the vegetation around the three lakes is broadly similar for the last 50,000 years and that pollen floras underwent parallel changes throughout this period.

The species that characterize Axis 1 are *Ludwigia*, and *Cassia* at its negative extreme and *Mauritia*, *Sagittaria/Echinodorus*, *Urticaceae/Moraceae* and *Cecropia* at its positive extreme (Fig. 7). On the second axis *Urticaceae/Moraceae* and *Cecropia* characterize the negative extreme while *Ilex* and *Mauritia* characterize the positive extreme. The first axis is largely driven by the type of fringing swamp at the lake margins. In samples that lack *Mauritia*, strong affinities are shown to other samples from the same

lake. Dragão currently lacks any fringing swamp vegetation, and this appears to have been a consistent pattern in the past. Dragão samples are neutral on Axis 1, but achieve some separation on Axis 2 (Figs. 7 and 8). The earlier Pleistocene samples (75–55 cm; >45,000–40,000 cal. BP) cluster together as do the late Pleistocene samples 50–35 cm; 20,000–14,000 cal. BP). Samples 30–5 cm (13,000–present) probably do form a distinct group, but because of much lower pollen concentrations, and small count sizes (100 grains or less) this group is statistically noisy.

The broad pattern among the Pata samples is that older samples are neutral on Axis 1, while the younger samples have strongly positive scores (Figs. 7 and 8). There is no consistent spatial separation among the Pleistocene aged samples from Pata (190–63.5 cm; ca. >45,000–17,000 cal. BP). However, the terminal Pleistocene and early Holocene are represented by a cluster of samples (63.5 and 55 cm; ca. 16,000 and 7000 cal. BP). Notably, a single sample at 60 cm (ca. 13,000 cal. BP) is anomalous in that it plots among samples from an earlier, cold (below) period.

The boundary between samples of the early and late Holocene in Pata is marked by another strong ecological change. The only sample in the Pata record with a positive value on Axis 2 is the sample from 50 cm depth (ca. 7000 cal. BP). Rich in both *Ilex* and *Mauritia* pollen grains, this sample plots close to the *Mauritia*-rich samples of Verde. However, the remainder of the late Holocene samples from Pata are ecologically distinct from all other samples in that they are rich in *Mauritia* and *Cecropia* but lack *Ilex*.

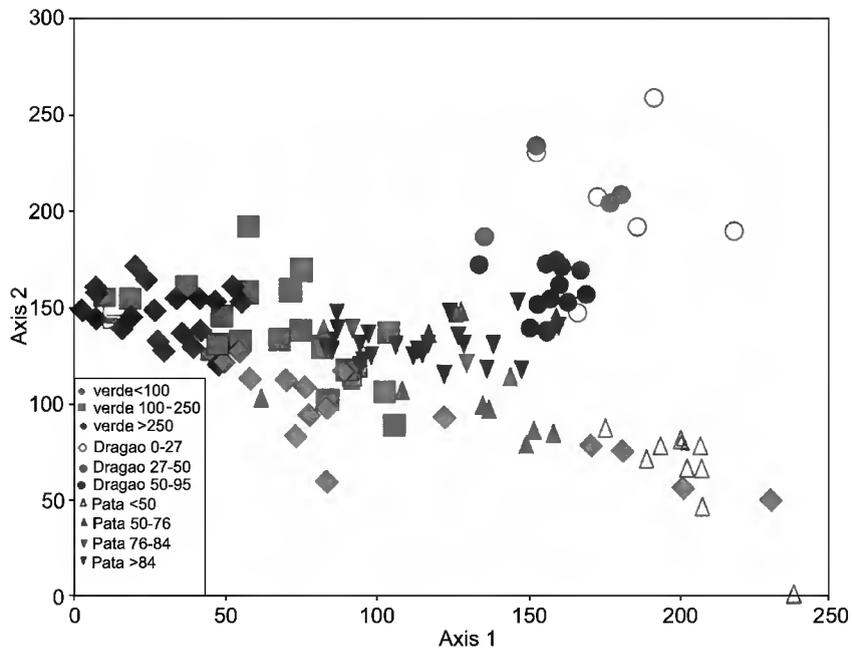


Fig. 7. Detrended correspondence analysis (DCA) results of sample data for the 24 most common fossil pollen types identified in the sediments of Dragão, Pata and Verde. Clustering of samples reflects zonation adopted in description of fossil pollen data.

The Verde samples (Pleistocene only) span almost the entire range of variation on Axis 1. Samples predating 25,000 cal. BP (460 cm and 200 cm; ca. >50,000–25,000 cal. BP) cluster with negative values

on both the first and second axes (Figs. 7 and 8). Samples between 175 and 45 cm (ca. 25,000–20,000 cal. BP) form a separate cluster that is slightly negative on Axis 1 and neutral on Axis 2. *Mauritia*

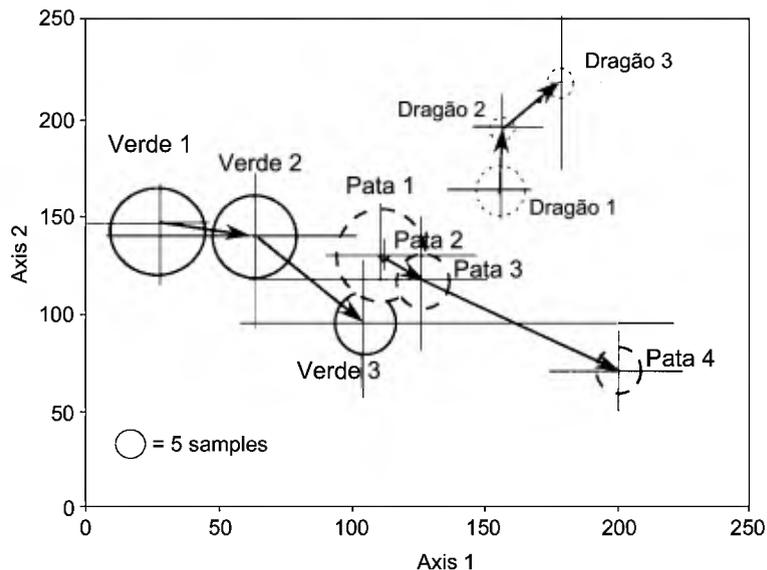


Fig. 8. Summary diagram of detrended correspondence analysis (DCA) results of sample data for the 24 most common fossil pollen types identified in the sediments of Dragão, Pata and Verde.

pollen became abundant within the Verde record late in the Pleistocene causing a trend in sample scores toward the positive extreme of Axis 1 (samples 40 to 25 cm; ca. 20,000–17,000 cal. BP). The sudden decline of *Mauritia* and the overall pollen signature of the forest cause the uppermost samples of the Pleistocene (10–0 cm; ca. 14,000 cal. BP) to be plotted close to those of the mid-Pleistocene.

4.6. Zonation

For three reasons we have adopted a simple regional zonation rather than using local pollen zones. The reasons are:

- (1) the three sedimentary records represent different portions of the late Quaternary and the adoption of an overall zonation makes it easier to compare across records;
- (2) the clustering of samples in the statistical analysis suggest that appropriate zone boundaries might be drawn at >45,000 to 22,000 cal. BP, 22,000 to 12,000 cal. BP and 12,000 to 0 cal. BP;
- (3) gross changes in depositional environments suggest a fourth discrete phase, that of 35,000 to 27,000 cal. BP.

Consequently, we have adopted a zonation that divides the records into four time periods: the mid-glacial (>45,000 to 35,000 cal. BP), the full glacial (35,000 to 27,000 cal. BP), the late glacial (22,000 to 12,000 cal. BP), and the Holocene (post 12,000 cal. BP).

In the following sections palynomorph diversities are provided, but to eliminate observer bias these should be compared only within cores and not between cores.

4.6.1. The early to mid-glacial (>45,000 to 35,000 cal. BP)

4.6.1.1. Dragão 1 (97–50 cm). Between 50 and 60 cm a gradual transition took place between a lower section of dark brown gyttja to an overlying section of dark yellow, nodular, gyttja. Both the lower section and the transitional zone date to the mid-glacial. Sediment accumulation rates were very slow approx-

imating to 0.0027 cm year⁻¹. The sediments are 20–30% organic content by mass.

Pollen concentrations are high with 100,000 to 150,000 pollen grains cm⁻³ (Fig. 9). Palynomorph diversity tracks pollen concentration and is extremely high with >110 pollen types identified in two of the samples within this zone (Fig. 9). In most samples arboreal pollen account for 80% of pollen input and lianas for a further 15% (Fig. 10). The most abundant arboreal pollen types are *Alchornea*, Euphorbiaceae, *Ilex*, Melastomataceae/Combretaceae, *Pouteria* type, and Urticaceae/Moraceae. Also present are taxa usually taken to be cold-climate indicators: Ericaceae, *Humiria*, *Myrsine*, and *Podocarpus*. Poaceae were present at 1–2% of the pollen sum (hereafter simply %).

4.6.1.2. Pata-1 (164–84 cm). Sediments are a blue-black gyttja that accumulated at a rate of approximately 0.01 cm year⁻¹. Pollen concentrations in Pata-1 were fairly high with values ranging from 150,000 to 300,000 grains per cm³ (Fig. 11). Palynomorph diversity varied between 33 and 56 types with a modal value of 43 types. Arboreal pollen was always >60% of the total pollen and usually >80% (Fig. 12). The most common taxa were Anacardiaceae, *Alchornea*, *Cassia*, *Copaifera*, *Ilex*, Melastomataceae/Combretaceae, Myrtaceae and Urticaceae/Moraceae. Cold-climate indicator taxa Ericaceae, *Humiria*, *Myrsine*, *Podocarpus*, *Weinmannia* were present throughout this interval. Poaceae were consistently rare, accounting for 1–2%.

4.6.1.3. Verde-1 (450–250 cm). The basal 50 cm of the core was a very stiff dark gray or black gyttja and this was overlain by a khaki gyttja that was slightly less compressed. Small black particles, probably limonite, occurred at concentrations estimated to be > 4 million per cm³. The accumulation rate of the blackest gyttja is unknown as it is all radiocarbon infinite in age. The khaki gyttja accumulated at a rate of 0.03 cm year⁻¹. This rate is very slow, but is an order of magnitude faster than the accumulation rate in Dragão and 3x faster than that of Pata. These sediments are highly organic (30–70% organic content by mass) but at about ca. 290 cm organic carbon concentrations fell abruptly, reaching a low for the entire core of 9.29% at 270 cm.

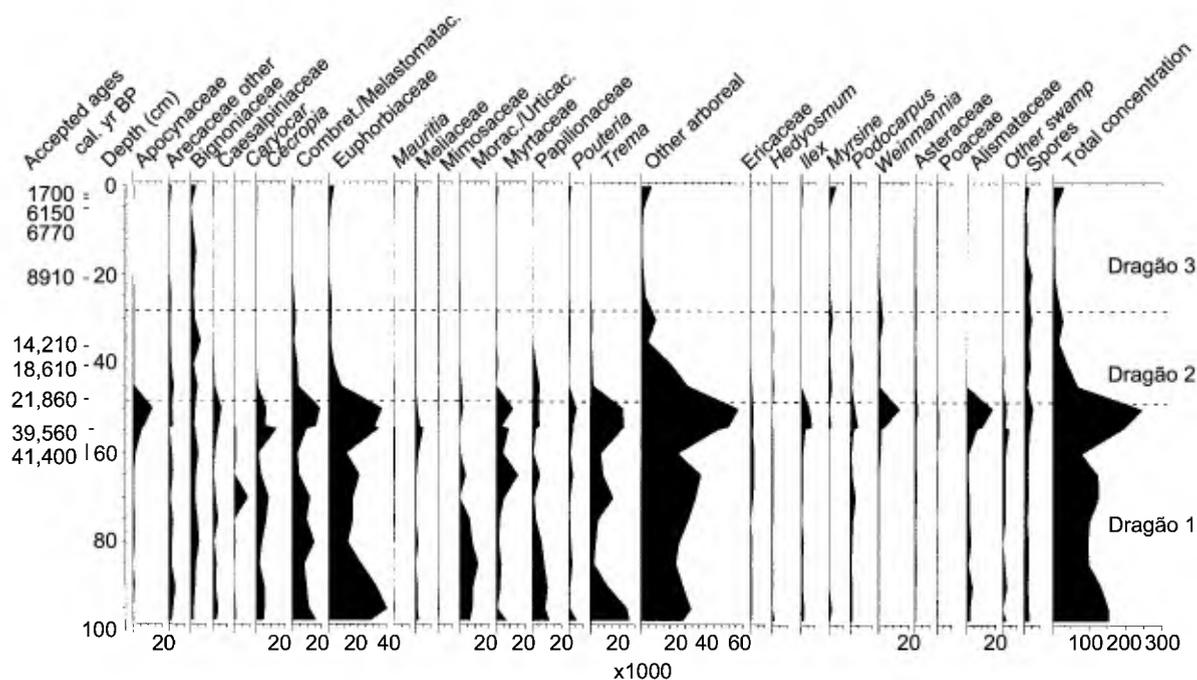


Fig. 9. Fossil pollen concentration data for selected taxa from Lake Dragão, Brazil.

Pollen concentrations in the basal gyttjas were extremely high with values $>1,000,000$ grains per cm^3 for most of this zone (Fig. 13). Between 350 and 250 cm pollen concentrations decline, suggesting a more rapid rate of sedimentation. Palynomorph diversity was also high with as many as 61 types recognized in the sample from 415 cm depth. In overlying sediments, palynomorph diversity declines but generally lies within the range of 35 to 50 taxa in each sample. Unlike Dragão, palynomorph diversity does not seem to be strongly related to pollen concentration in this or subsequent zones in the Verde record. The percentage of arboreal taxa was $>80\%$ with the same assemblage of common species and cold-climate indicator taxa as documented in Pata (Fig. 14). Poaceae were consistently present at 1–3% of the pollen count.

4.6.2. The full glacial (35,000 to 22,000 cal. BP)

4.6.2.1. Dragão 2. No sediment accumulation.

4.6.2.2. Pata 2 (84–76 cm). This period was represented by a nodular yellowish clay that was deposited very slowly (0.00002 cm year $^{-1}$). Indeed,

this rate of deposition was so slow that it may well have occurred as a series of stop-and-start episodes.

Two pollen samples were analyzed from this section of the core and both had very high pollen concentrations ($600,000$ and $800,000$ grains cm^{-3}). Such high concentrations were consistent with a very slow accumulation rate, and suggest that the sediments were not dry enough to be fully oxidized. A mean of 48 taxa were recognized per sample. The pollen spectrum of this zone was similar to that of Pata-1 (see above list for common and cold-tolerant taxa) with $>80\%$ of pollen derived from arboreal taxa. All the common taxa listed in the previous section were present in Pata 2 and there were many rare elements including: *Apeiba*, *Caryocar*, *Cassia*, *Cedrela*, *Celtis*, *Cissus*, *Cordia*, *Dalbergia*, *Lacmellea*, *Macrolobium*, *Mauritia*, *Monstera*, *Pouteria*, *Protium*, *Psychotria*, *Sebastiania*, *Schefflera*, *Tabebuia*, *Tapirira*, *Trattinickia*, *Vochysia*, and *Cyathea*ceae. Pollen grains of Poaceae (3%) and herbaceous taxa remained rare.

4.6.2.3. Verde 2 (250–100 cm). Coarsely laminated gyttjas characterized this zone. Sedimentation rate

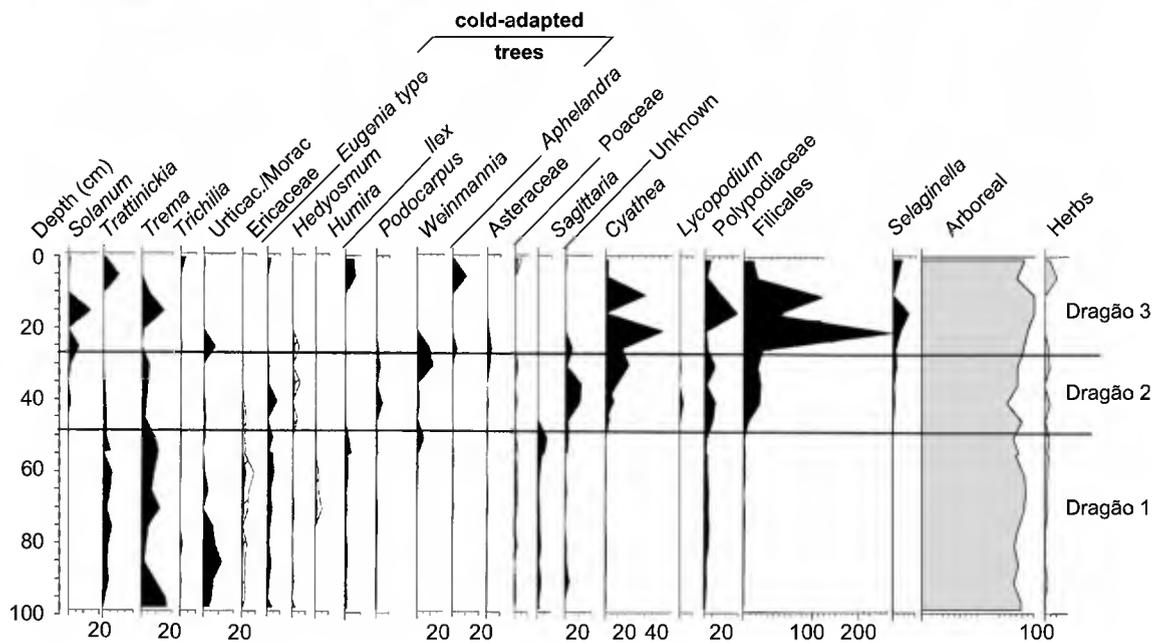
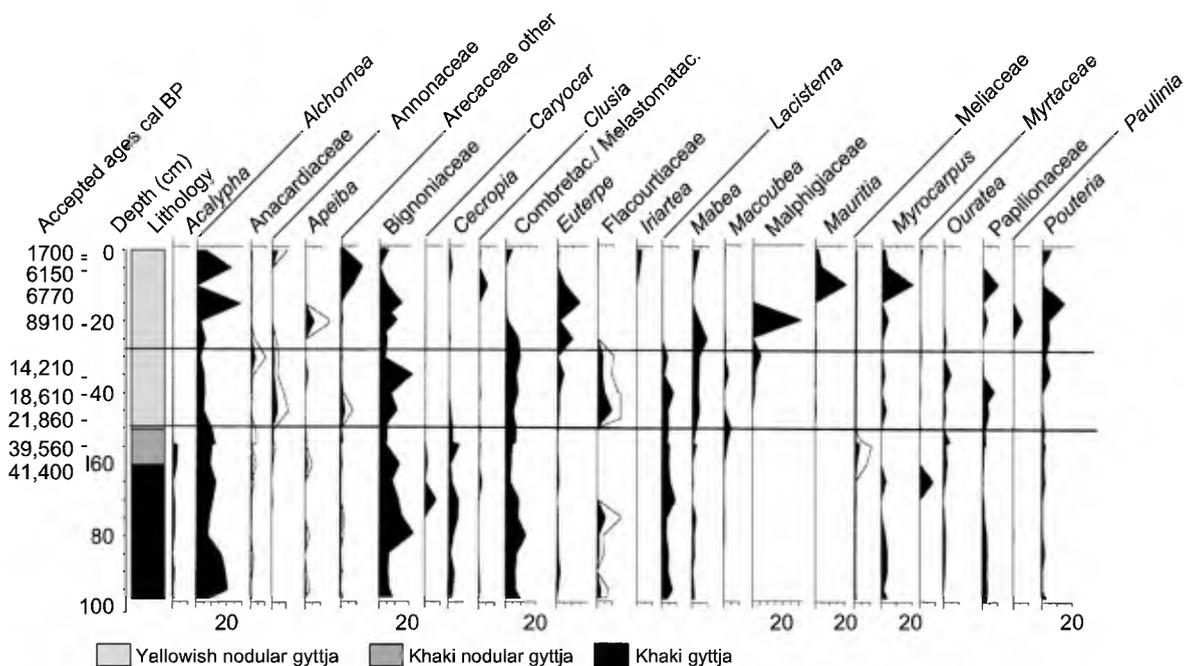


Fig. 10. Fossil pollen percentage data for selected taxa from Lake Dragão, Brazil.

varied due to a sudden acceleration of deposition after ca. 20,000 cal. BP. The sedimentary rate within the early part of this zone is about 0.015, but through the later stage of this zone deposition increases by a factor

of 10 to 0.17 cm year⁻¹. Sedimentary carbon content is constant at ca. 12%.

The lowest pollen concentrations (mean=3758 grains cm⁻³) of the core were recorded between 145

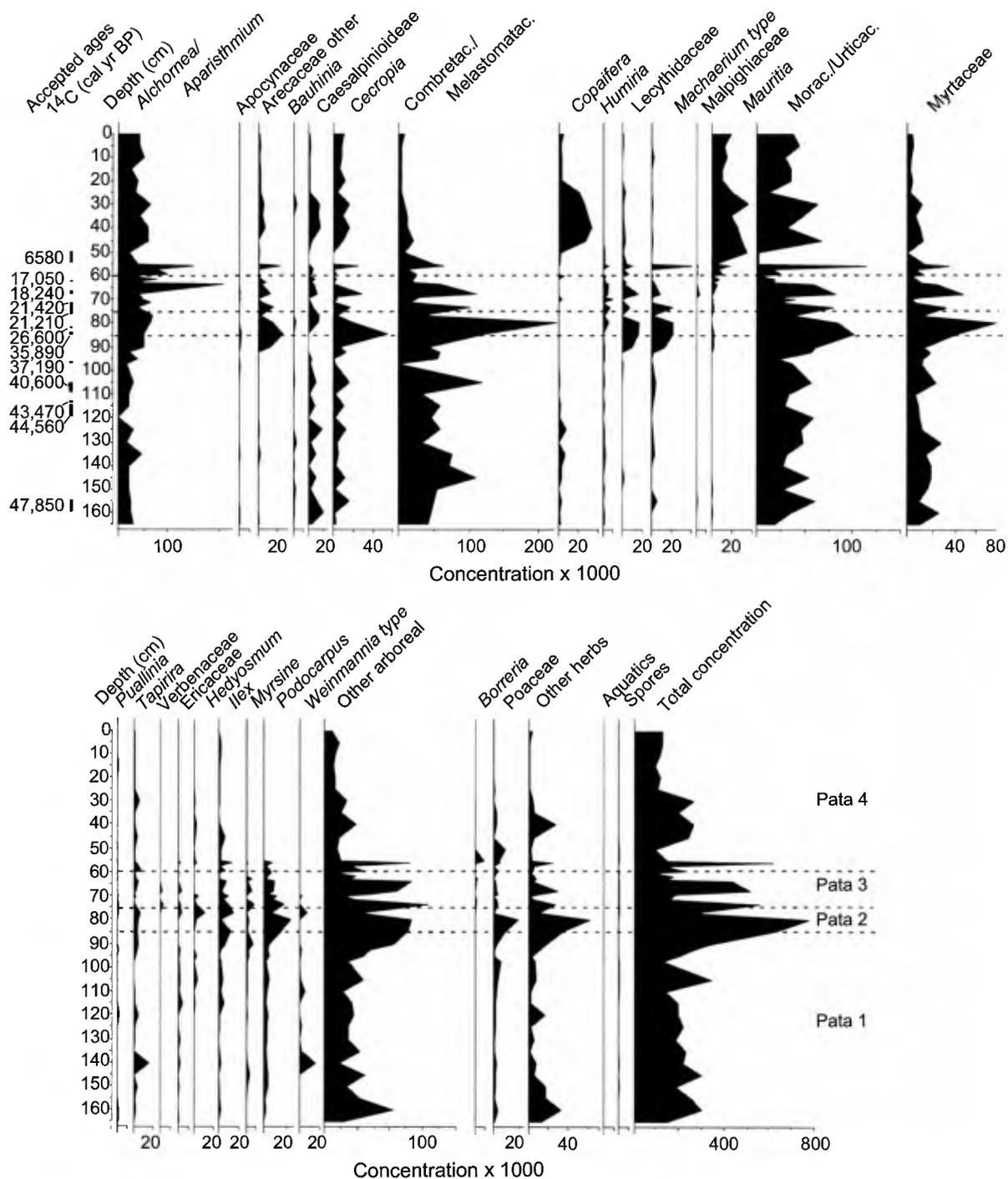


Fig. 11. Fossil pollen concentration data for selected taxa from Lake Pata, Brazil.

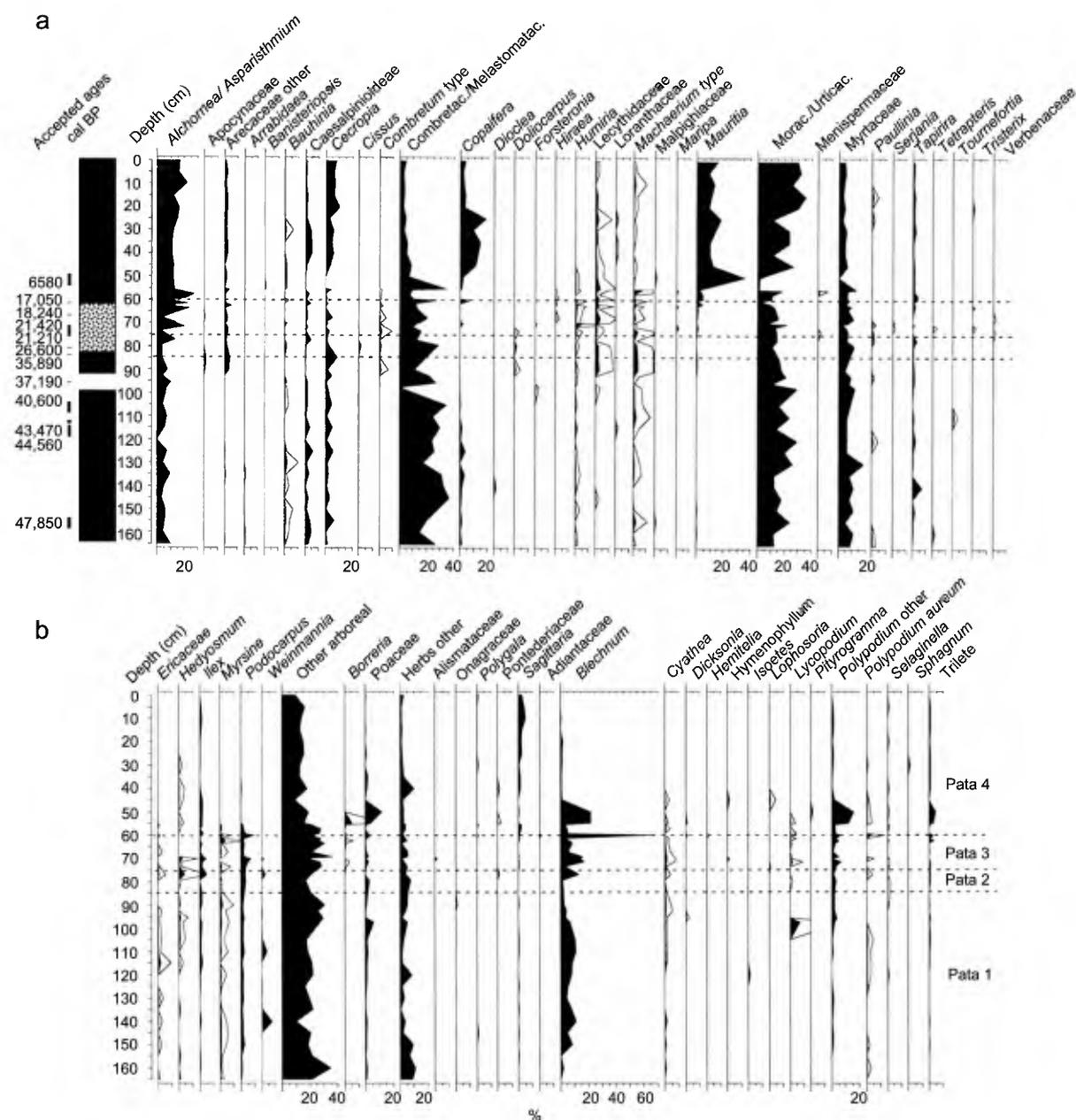


Fig. 12. Fossil pollen percentage data for selected taxa from Lake Pata, Brazil.

and 185 cm depth (ca. 23,000–27,000 cal. BP). An unidentified colonial alga (ca. 10 μm in diameter) became abundant during this interval. Typical algal cell concentrations were 5000–20,000 algal cells cm^{-3} , but the sample at 152 cm was a pure algal mud with an estimated 80 million algal cells cm^{-3} .

Pollen recovery from the sample at 152 cm depth was poor, but in other layers within this zone the modal concentrations of pollen generally lay between 50,000 and 100,000 grains cm^{-3} . Palynomorph diversity increased steadily throughout this zone, reaching a maximum of 57 taxa at 155 cm. Thereafter, diversity

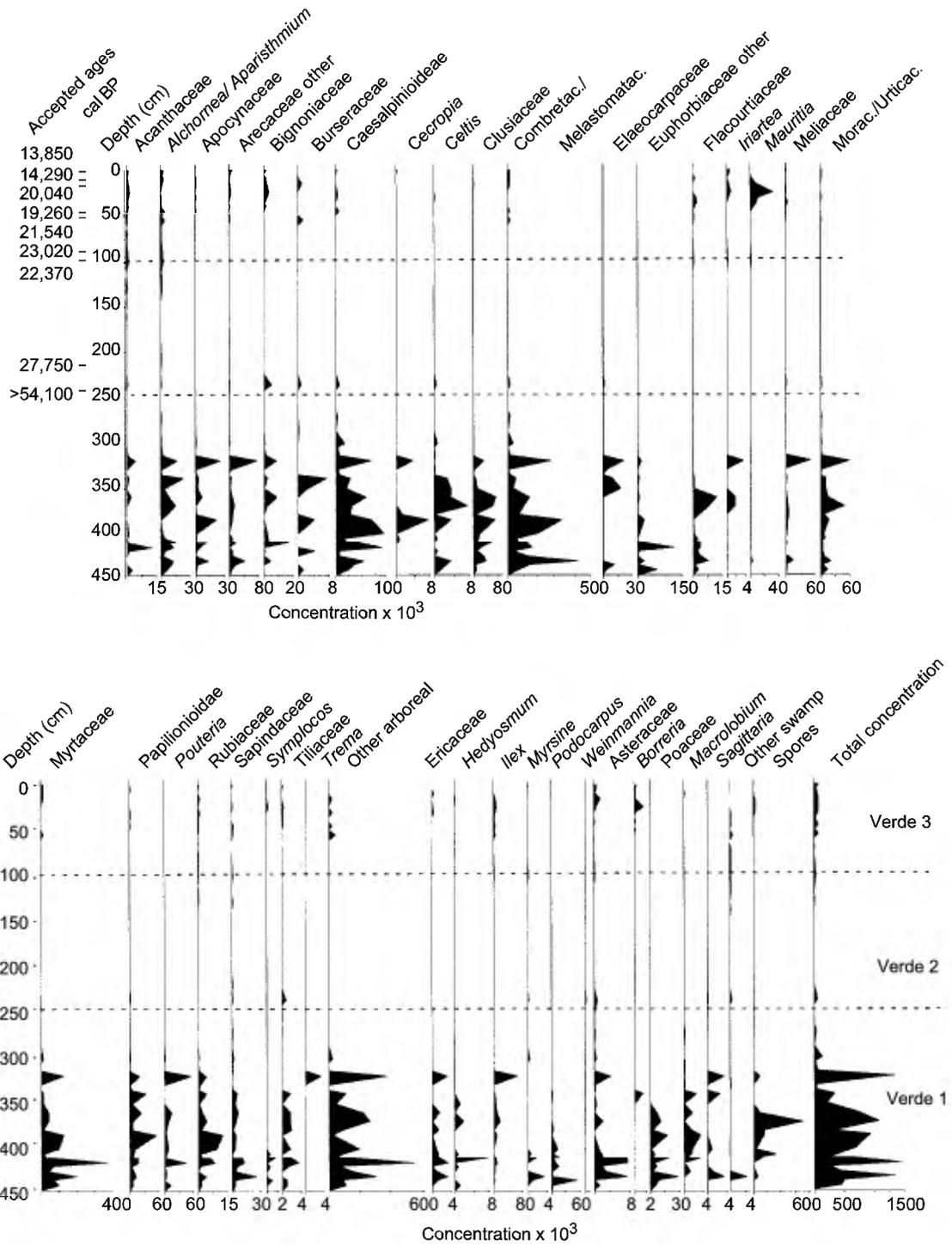


Fig. 13. Fossil pollen concentration data for selected taxa from Lake Verde, Brazil.

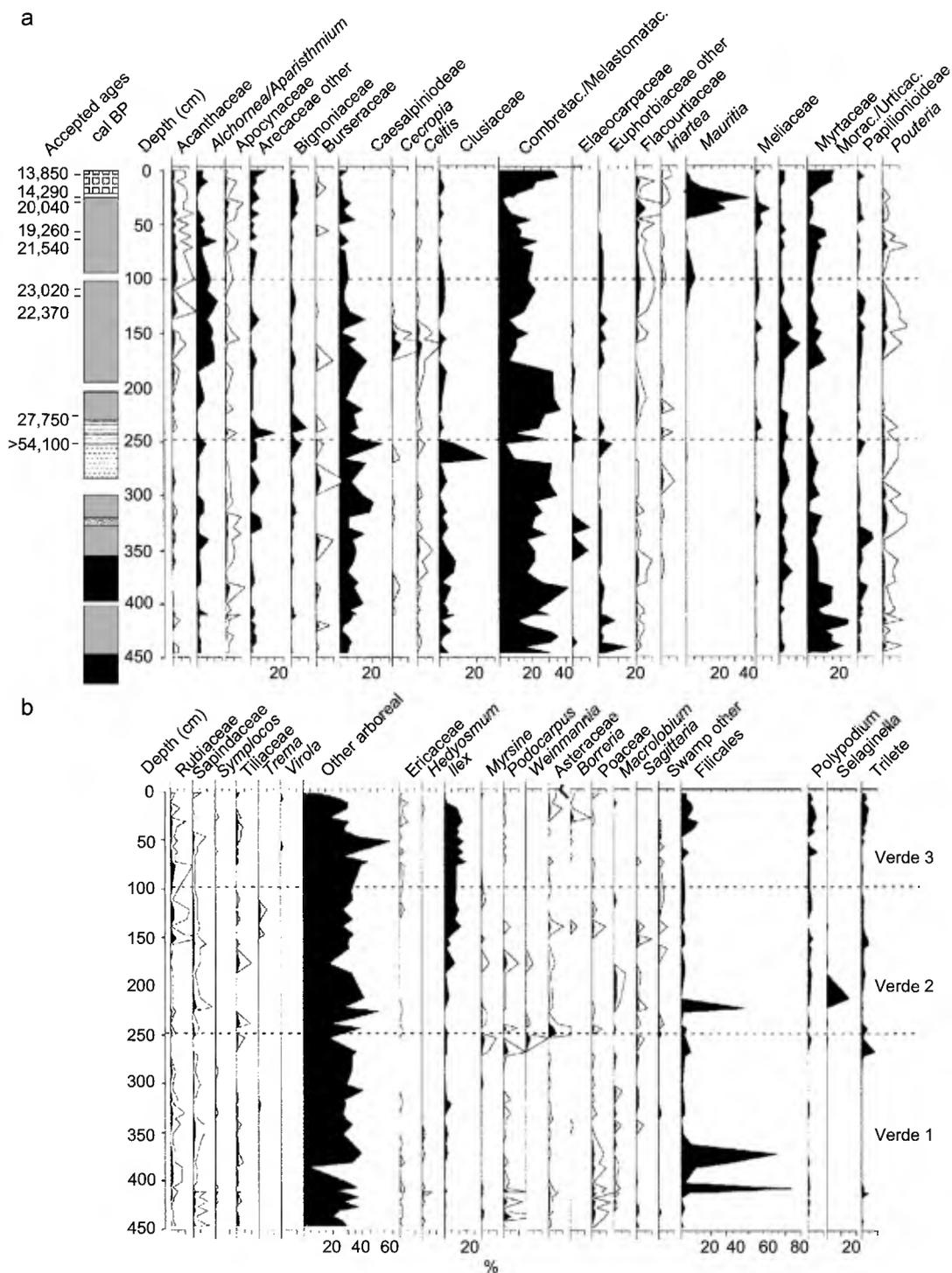


Fig. 14. Fossil pollen percentage data for selected taxa from Lake Verde, Brazil.

lay within the range of 45 to 56 palynomorphs per sample.

No matter whether the sediment samples were rich or poor in pollen, the basic composition of the pollen spectra was constant. Arboreal taxa produced >80% of pollen counted in all levels. Melastomataceae/Combretaceae, *Clusia* and *Cassia* were among the most common arboreal types, but the rarer taxa provide more insight into the type of forest surrounding the lake. *Alchornea*, *Aphelandra*, Bignoniaceae, *Caryocar*, *Cedrela*, Chrysobalanaceae, *Guarea*, *Ilex*, *Iriarte*, Lecythidaceae, *Mabea*, *Podocarpus*, *Pouteria*, *Rhodognaphalopsis*, *Sapium*, *Trichilia*, Urticaceae/Moraceae, are present in these spectra, and all of these are forest elements. Asteraceae show a brief increase at ca. 28,000 cal. BP, but it should be noted that the modern forest contains arboreal Asteraceae such as *Vernonia*, and many vining composites, such as *Mikania*, occupy lake edge habitats. Poaceae do not exceed 3%.

4.6.3. The late glacial (22,000–12,000 cal. BP)

4.6.3.1. *Dragão 3 (50–27 cm)*. Sediments of this zone are nodular yellow clays that were deposited at a rate of ca. 0.0029 cm year⁻¹. Organic content of the sediments increases to about 35% dry weight.

Pollen concentrations are much lower than in *Dragão 1* and decline from ca. 50,000 grains cm⁻³ at the base of the zone to about 5000 grains cm⁻³ at the top of the zone. There is a similar loss of palynomorph diversity from 80 palynomorphs per sample at the base to 35 types at the top of the zone. Nevertheless, the basic signature of a forest flora is constant both within the zone and when compared with *Dragão 1*. In *Dragão 3*, >65% comes from arboreal taxa and a further 15–20% comes from lianas. Pollen of *Podocarpus* (7%) and *Myrsine* (3%) attain their peak abundance in this zone while Poaceae and herbaceous elements are rare (<2%).

4.6.3.2. *Pata 3 (76–60 cm)*. Nodular yellow clays that had an accumulation rate of 0.002 cm year⁻¹ end abruptly at 60 cm with the onset of deposition of a soft black gyttja. The pollen concentrations of this sedimentary unit remain high as does palynomorph diversity. Sixty-three palynomorphs are identified in the basal sample of this zone, thereafter diversity is

fairly stable at around 48 palynomorphs per sample. One low value of 32 types was documented at 63.5 cm but there is no other indication that this sample was unusual. This zone is marked by the highest values of *Hedyosmum*, *Humiria*, *Ilex*, *Myrsine*, and *Podocarpus*, and an overall abundance (>80%) of forest taxa. Some thermophilous mesic elements such as *Alchornea* and *Mauritia* start to increase in abundance at the end of this zone.

4.6.3.3. *Verde 3 (100–0 cm)*. The khaki gyttjas of *Verde 3* were deposited at a rate of ca. 0.17 cm year⁻¹, but apparently 0 cm depth equates to 14,000 cal. BP. The organic content of samples in this zone falls from 10.2% to 9.6% between 100 and 40 cm, before rising to 12.5% of dry mass. The pollen concentrations in these samples are high with >1,000,000 grains cm⁻³ in most samples. Palynomorph diversity is relatively constant at around 48 types per sample. As in previous samples, arboreal taxa predominate and this zone is marked by the increased abundance of *Alchornea*, *Ilex*, *Mauritia*, *Myrtaceae*, and *Trichilia*.

4.6.4. The Holocene (post 12,000 cal. BP)

4.6.4.1. *Dragão 4 (27–0 cm)*. The nodular yellow clays that form the Holocene sediment had accumulation rates of between 0.004 and 0.002 cm year⁻¹. Despite these very slow accumulation rates the organic content of these sediments reaches >50% of the dry weight.

Pollen concentrations in the Holocene sediments of *Dragão* are low with between 2000 and 30,000 grains cm⁻³. The diversity of palynomorphs was low with between 8 and 45 types identified in each sample, with the lowest diversity corresponding to pollen counts of <100 grains.

Arboreal pollen types accounted for 60–75% of all pollen counts, with lianas (2–10%) and unknown grains (10–20%) accounting for the majority of other types. The most abundant arboreal pollen types were: *Alchornea*, Cyatheaceae, *Ilex*, *Mabea*, Melastomataceae/Combretaceae, *Pouteria* type, *Sapium*, and Urticaceae/Moraceae occurring commonly (Fig. 10). Poaceae never exceeded 10%.

4.6.4.2. *Pata-4 (60–0 cm)*. The Holocene sediments of *Pata* are soft black gyttjas that were deposited at a

rate of between 0.01 and 0.0024 cm year⁻¹. However, the early Holocene appears to have had much slower deposition compared with more rapid rates in the late Holocene. Most pollen samples in this zone have concentrations of between 100,000 and 250,000 grains cm⁻³. However, the early Holocene is marked by very high pollen concentrations that exceed 600,000 cm⁻³. Such high concentrations are consistent with very slow rates of sediment accumulation. Arboreal pollen is >80% of the total pollen count in all samples and generally exceeds 90%. An unknown pollen type, a small tricolporate reticulate grain occurred as a rare component in many samples, but reached a peak occurrence of 55% in a single mid-Holocene sample. We regard the most likely source for this palynomorph to have been an as yet unidentified bankside tree. *Cecropia*, *Copaifera*, and *Mauritia* became abundant for the first time and provided a sufficiently unique character that samples within this zone are isolated in the DCA results. The most common trees identified in this zone were: *Alchornea*, *Ilex*, Melastomataceae/Combretaceae, *Pouteria* type, *Sapium*, *Trichilia* and Urticaceae/Moraceae. Poaceae were generally <2%, but in one mid-Holocene sample their representation reached 8%.

4.6.4.3. Verde. No Holocene record.

We believe that the lack of a Holocene record at Verde is a coring artifact resulting from inadvertently penetrating and failing to collect unconsolidated Holocene sediments.

5. Discussion

5.1. Interpretation of the palaeochemical record

The most distinctive signal in these data sets is the cyclic nature of the K⁺ peaks in the Pata core (Bush et al., 2002). Peak concentrations of K⁺ are an order of magnitude higher than those of intervening troughs. The ultimate origin of K⁺ in this system should be release from the intrusive plutonic feldspars and mica that form the catchment. However, the lack of coupling in the magnitude of variation between K⁺ and Na⁺ suggests that the periodicity cannot be a simple consequence of fluctuating erosion. Relative

concentration of K⁺ in the sediments, therefore, should depend on processes that periodically concentrate K⁺ but not Na⁺ within the lake system itself. We propose that K⁺ is concentrated by planktonic and benthic algae at times when productivity is enhanced by lowered lake level. The K⁺ maxima record long episodes of shallow ponding when K⁺ is concentrated by the biota from the cations mobilized from the sediment body by changes in redox potential. K⁺ minima denote times, like the present, when the lake is usually several meters deep with poor light penetration, low primary productivity, and hence low concentration of K⁺ by the biota.

Qualitative data consistent with this hypothesis are found in the gross stratigraphy of the sediments and in the evidence of algal remains. Intervals of nodular clays correspond closely with K⁺ maxima (Fig. 4). Nodular clay layers contained vast numbers of algal cysts (>4 million cells cm⁻³) that may belong to the genus *Scenedesmus*. Other sections of the core contained 0–1000 *Scenedesmus* cells cm⁻³.

Lake Pata, like other pseudokarst lakes of the “Six Lakes Hill” inselberg, probably has its water level determined by seepage as well as changes in precipitation. Lake Dragão on the inselberg lost >1 m of water in a 2-week period in, 1991. Videotape of Pata clearly shows that all bankside trees have twigs terminating about 1m above the observed water-level. Staining of bankside rocks and this apparent “pruning” strongly suggest that during wetter phases of the year, lake level in Pata rises by ca. 1 m. No such evidence of variation was evident in neighboring Verde. As the lowering of lake level in was clearly too fast to be accounted for by evaporation we hypothesize that these basins are incompletely sealed. Probably, the principle loss of water from Pata is associated with its deep fissure, not with evaporation. That periods of low lake level are not the result of increased evaporation is consistent with the absence of Na⁺ enrichment. As long as rainfall is roughly constant throughout the year, a relatively deep lake is maintained; but the system is vulnerable to modest reductions in precipitation, possibly requiring no more than reduced rainfall in the nominal wet season (DJF).

K⁺ data are lacking for sufficient samples in the 22,000–37,000 cal. BP range because extremely low sedimentation rates over this interval make our

sampling interval inadequate. A working hypothesis to explain times of lowered sediment accumulation is that ponding was reduced so that the lake was ephemeral with consequent oxidation of non-pollen organic matter, while mineral inputs continued to be prevented by the intact vegetation cover. The consistently low values of SPDU are consistent with Pata having been a very shallow lake for much of its history.

Thus the low lake/high K^+ episodes at Pata are best explained as times when the delicate balance between influx from precipitation and seepage lowers lake level to the critical position that allows dense algal blooms.

The paleochemistry of Dragão was not investigated, though a lake lowstand at ca. 35,000 to 20,000 cal. BP is evident in the presence of nodular clays and the sedimentary hiatus. The Verde data for K^+ and Na^+ are more closely coupled than those of Pata (Fig. 5), and both cations are present at much lower concentrations in the sediment. The reason that Verde may not be as sensitive a meter of precipitation change is that its greater depth may have buffered it against the kind of lowstands evident in Pata. Consistent with this observation are the concentrations of SPDU that

indicate sufficient water depth to maintain an anoxic burial zone throughout much of this core. Variations in Fe and Mn can also be used as a crude proxy of anoxia, as high concentrations of Fe and Mn often correlate with the high redox potential found in sediments of relatively deep lakes. Despite being a deeper water body than Pata, there were sedimentary phases in Verde that have poor pollen preservation and an abundance of algal detritus. These zones, usually characterized by nodular material, align to the major peak of K^+ in the core at ca. 35,000 cal. BP.

The regular spacing of low lake stand events at Pata suggests a climatic forcing. Within the range of ^{14}C dating a peak of K^+ is evident at ca. 15,000 to 5000 cal. BP and we know that the lowest lake stand of all occurred between 37,000 and 27,000 cal. BP. A comparison of the K^+ data with orbitally induced changes in insolation (Milankovitch plots) at 0° latitude (Fig. 15) for June–July–August (JJA) and December–January–February (DJF) reveals a strong correlation of high lake level with the peaks of DJF insolation and low lake level with peaks of JJA insolation (Bush et al., 2002). Accepting the correlation between K^+ and insolation as causally connected we can extend the correlation to cover all eight peaks

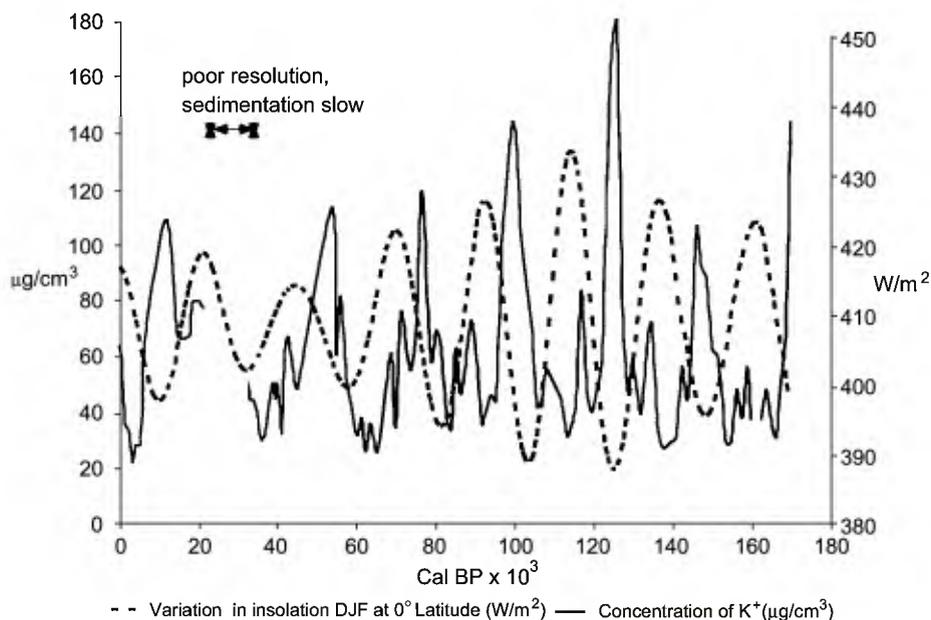


Fig. 15. Comparison of K^+ concentrations in sediments of Lake Pata, Brazil, with % departure from modern December–January–February insolation to 0° latitude. Insolation data derived using Analyseries 2.1 software (Paillard et al., 1996).

of K^+ . We aligned the last datum in the sequence with the insolation curve at 170,000 years BP. All intervening points assume a steady rate of sedimentation between 50,000 and 170,000 years ago. Clearly, the relationship between insolation and K^+ peaks is a crude approximation and cannot be used to address whether there are temporal leads or lags in the system. Nevertheless, the peaks of insolation are clearly correlated with peaks of K^+ . This chronology suggests that the Pata record spans two complete glacial cycles beginning at the onset of MIS 6.

5.2. *The role of the watersheds*

Given the proximity of these lakes, Dragão, Pata and Verde hold markedly different stratigraphic records. We hypothesize that because these lakes do not have uniform rates of leakage, the timing and intensity of lake level fluctuations differ. The deposition and sub-fossilization of organic material is strongly influenced by lake depth. In our experience, anoxia at the mud–water interface, the conditions needed for preservation of organic matter, is rare in lakes <1 m deep, but is usual in lakes >3 m deep. Thus, rate of organic build-up in lake sediments varies according to the probability that the time between sedimentary deposition and burial is spent in a reducing, or oxidative environment. Under saturated conditions, lake sediments are essentially anoxic once they are buried below the zone of biological activity. In deep tropical lakes, most waters beneath the thermocline are anoxic (Wetzel and Likens, 2000). However, if the lake is too shallow for stratification to develop, or if the lake is highly oligotrophic, even the mud–water interface may still be oxic (containing some oxygen). In such circumstances, the time taken from the moment of deposition to burial into anoxic layers (usually a few millimeters into the sediment) may be critical for the preservation of organic carbon, pollen grains and, especially, pigments. Principal factors determining this gradient of burial time are:

- (1) A lake with a high volume: surface-area ratio is less subject to evaporative drying.
- (2) A deep tropical lake is inherently more likely to have thermal stratification and anoxic bottom waters than a shallow one.
- (3) A lake with a high catchment area: lake surface area ratio is less subject to evaporative drying, because it receives a proportionately greater volume of runoff.
- (4) A large catchment is likely to yield more sediment than a small catchment, because catchment area is also the erodable surface area that supplies mineral sediment.
- (5) Biological productivity is positively correlated with deposition of detritus and hence inversely correlated with time between deposition and burial.
- (6) Evidence of an unstable local hydrology. Amount of leakage from an imperfectly sealed basin.

If the three lakes are contrasted on this basis, we observe that both Dragão and Verde are moderately deep, have small catchments, are highly oligotrophic. The principal differences between them appear to be the modern color of Verde and the extremely unstable hydrology of Dragão. Pata is shallow, has the highest catchment area: surface area ratio, is oligotrophic and appears to have a more stable hydrology. On this basis we suggest that Dragão has the greatest probability of sediment oxidation, Verde is probably the next most sensitive because of its small catchment area, and Pata may be the most stable of the group in terms of lake level fluctuations. We would predict that both Verde and Pata would exhibit intermittent sediment oxidation under extreme circumstances. That the lakes have different probabilities of maintaining a reducing environment goes a long way to explaining time-transgressive changes in gross stratigraphies.

We propose that the sedimentary histories of the lakes provide evidence of three distinct oxidative/reductive states within this lake system.

5.2.1. *Frequent oxidation of mud–water interface*

A common feature of lowland neotropical lakes that dry out during the dry season is that they fail to accumulate organic sediment. We have often arrived at a lake to find that it is not a permanent water body, lacks organic sediment, and has a clay bottom. In such lakes, where the lake evaporates and the clay bottom bakes dry, all carbon is lost from the system through oxidation. These lakes have a closed carbon cycle and pollen is not preserved in the sediment. The clays that

accumulate under these conditions are allochthonous, and the rate of deposition is a function of local environmental conditions, especially the bedrock, shape, size, steepness and vegetational state of the local watershed.

In all three lakes, a closed carbon cycle appears to have been established between 35,000 and 26,000 years ago (longer in Verde and Dragão). During these phases the lake would have contracted seasonally to a puddle in a flat-bottomed basin. The almost non-existent soils on the ironstone would have provided very little allochthonous material, and any soil washed off the surrounding rocks may have been trapped on the flat-bottomed bed of the lake. Under such conditions, allochthonous input would be trivially small and a closed carbon cycle in the lake bed would result in no net accumulation either of organic or inorganic material. However, it is important to note that the underlying sediments show no sign of oxidation. Clearly, oxidation was restricted to the surface layer. A close analog, in a very different setting, would be the Grenzhorizont horizons of European bogs (Moore et al., 1991), where there was no net accumulation, but because of a high water-table, reducing conditions were maintained in the underlying material. Thus it may be more helpful to think of these systems as shallow puddles that contain oxygen from top to bottom, rather than a truly dry lake-bed.

5.2.2. Infrequent oxidation of mud–water interface

A near-permanent lake that occasionally dries out accumulates an organic rich gyttja. However, these infrequent oxidation cycles are sufficient to change the coloration and consistency of clays. The resulting sediment is a nodular clay-rich gyttja with a high water content, high carbon content, and yellow-orange coloration. Each exposure event is not sufficient to oxidize subsurface layers, evidenced by the high percentage of organic matter in these samples.

For example, pollen preservation in Dragão is good in most levels, and the types of pollen preserved include large numbers of delicate forms, e.g. *Urticaceae/Moraceae*, *Cecropia* and *Miconia* type (the most common palynomorph grouped under *Melastomataceae/Combretaceae*). The presence of these grains and the absence of high percentages of types known to be rich in sporopollenin, e.g. spores, *Poaceae* and

Asteraceae, suggest that there has not been selective preservation of pollen grains in these sediments. Further confidence in the integrity of the pollen record comes from a comparison of the spectra of common pollen types in Dragão, with those of Pata and Verde (which were wet during the late Pleistocene and Holocene). In all three records the basic components of the pollen rain are the same; observed variation between the records is due to the expected local variance in forest composition.

We suggest that at Dragão, water levels have oscillated throughout the late Pleistocene and Holocene. After 22,000 cal. BP, sediments of Dragão reflect a lake in which the mud–water interface is occasionally oxic. We note that the Dragão pollen concentrations are lowest during the mid-Holocene and increase in the late Holocene. Where low pollen concentrations co-occur with low palynomorph diversity we infer a more profound drying that caused some oxidation of pollen. If that observation is true, this trend suggests that the mid-Holocene was a time of increased seasonality or decreased moisture availability. In the last 5000 years increasing pollen concentration suggests less frequent drying of the site.

Compaction by overlying sediment reduces the water content of these clay-rich gyttjas and results in the formation of a dense nodular yellow sediment. Such a sediment is found in Verde between zones 1 and 2 and in Pata zone 2. We suggest that the volatility (not the depth) of the modern lake system at Dragão offers an approximate analog for the hydrological conditions of Verde and Pata between 35,000 and 26,000 years ago.

5.2.3. Permanent reducing environment at mud–water interface

In lakes that maintain reducing conditions, but in which there is almost no allochthonous mineral input, rates of sediment accumulation are extremely slow. Steep basin sides and relatively deep basins restrict the establishment of submerged aquatics. Consequently, inputs of autochthonous organic material are dominated by algae. In the extremely nutrient poor waters of Dragão and Pata, algal productivity is extremely low. In Verde, where algal blooms color the water, deposition is faster. A phase of relatively rapid sedimentation in Verde is suggested at ca. 20,000 cal. BP when dense algal blooms contributed more sedi-

ment than at any other time. SPDU are a measure of chlorophyll pigments preserved within the sediment. SPDU are likely to be highest in shallow lakes where nutrients are concentrated. However, if the lake does not have anoxic bottom waters, the pigments are oxidized. Thus the SPDU are particularly useful for identifying shallow productive systems (high values), and periods when a lake becomes so shallow that the mud–water interface is occasionally oxic (zero values). Zero or very low values of SPDU can also be recorded when a lake is deep and unproductive. Low Redox sensitivity (i.e. low concentrations of Fe and Mn) can be used to distinguish a shallow system from a deep one, and thus determine whether low SPDU values are caused by oxidation or lack of productivity. As Pata is so shallow it is not surprising to find that it has not retained a pigmentary record. Verde on the other hand has a complex history that can be interpreted in terms of SPDU and redox.

Some observations based on the palynological record also shed light on the status of the water bodies. The rarity of elements such as *Symphonia*, *Iriartea*, *Macrolobium*, *Genipa*, and *Pachira*, and low abundances of Poaceae and Cyperaceae, suggest that an extensive swamp never formed at these sites. The principal element that we interpret to be an indicator of swamp conditions in this record is *Mauritia*.

Mauritia is a prolific pollen producer and in some Amazonian records this palm can exceed 70% representation (Bush et al., 2001). However, *Mauritia* never achieves this level of dominance in the records from the Hill of Six Lakes. *Mauritia* is only found in a single level at the start of the Holocene in Dragão, but in the two lakes that currently support some *Mauritia*, it is a more important component of the fossil record. In Pata, *Mauritia* is present, but rare, in zones 1 and 2. At, or shortly before, the Pleistocene/Holocene boundary *Mauritia* increases in importance and thereafter is consistently present at 10–15%. In Verde, *Mauritia* is rare until the terminal Pleistocene when a *Mauritia* swamp develops close to the site. *Mauritia* requires saturated soils, but seldom grows in permanently flooded settings. *Mauritia* forests do not establish on systems with closed carbon cycles, and our observation is that they usually generate substantial deposition of organic matter that decays to a coarse peat. As these sedimentary sequences contain neither peaty lenses, nor very abundant *Mauritia*

pollen, it is probable that *Mauritia*, though present, could not invade the bed of the lakes.

In Verde, the peak of *Mauritia* pollen abundance (37%) coincides with an increased abundance of all categories of fern spores. The *Mauritia* may not have grown at the site at an earlier time because it was too cold (below) and its brief presence in the late Pleistocene may represent a warm phase when lake levels were low enough that *Mauritia* could invade the lake margin. The disappearance of *Mauritia* in the uppermost levels of the Verde sequence could reflect either the flooding of all suitable habitat as lake level rose, or it could reflect a resumption of cold conditions.

It is not possible to quantify the changes in precipitation experienced during the Pleistocene at the Hill of Six Lakes, beyond observing that the change in moisture availability was enough to cause a lake that was 2 m deep to dry out cyclically, but only one event between ca. 35,000 and 26,000 cal. BP was strong enough to allow lake level to drop in all three basins. None of these events was strong enough to remove forest cover from this edaphically dry landscape.

5.3. Three forest records

The aggregate inference that can be made from these three pollen records is that forest was continuously present at, and around, the Hill of Six Lakes during the last 50,000 years. Given some previous Amazonian pollen spectra of Pleistocene age (Absy et al., 1991; van der Hammen, 1974) in which Poaceae pollen are abundant and forest taxa decline to 20%, the constant representation of arboreal taxa at the Hill of Six Lakes is striking. Despite the different durations of sedimentary hiatuses in these records, there is no marked change in the pollen spectrum that marks the discontinuity. Note how the sample scores of zones 1 and 2 are overlapped in the DCA analysis from Verde. Although as zone 1 may be 20,000 years older than zone 2 there is no distinct change in forest composition, suggesting remarkable stability. A finding that is entirely consistent with data from a continuous lower montane Pleistocene record from Peru (Bush et al., 2004). Although the fossil pollen spectra of the Pleistocene differ in species composition from those of the Holocene, these records

indicate that this inselberg remained forested (Colinvaux et al., 1996). Poaceae and charcoal, the great indicators of an opening of forests are rare throughout. Poaceae never exceed 5%, a proportion that we have earlier suggested is typical of closed forest environments (Bush, 1991; Bush and Colinvaux, 1988; Bush and Rivera, 1998).

In temperate regions the concept of Pleistocene no-analog communities (Davis, 1981, Webb, 1987) and no analog climates (Jackson and Overpeck, 2000) has replaced the more static view of closely co-evolved communities. In the tropics, there have been few opportunities to test whether Pleistocene communities were similarly without modern parallel. At El Valle, Panama, Bush and Colinvaux (1990) showed the co-occurrence of the montane element *Quercus* and lowland taxa such as *Luehea*, *Trema*, Urticaceae/Moraceae, and various Arecaceae. Similarly, at Mera and San Juan Bosco, Ecuador, montane and lowland elements mixed prior to the LGM in the foothills of the Andes (Bush et al., 1990). Comparable no-analog communities have been suggested within lowland Amazonia, both in the original study of Lake Pata sediments, and for a lake on the similar inselberg of Maicuru in eastern Amazonia (Colinvaux et al., 1996, 2001), but these have not yet been extensively documented.

The evidence for a no-analog community at the Hill of Six Lakes comes from the occurrence of mixed montane and lowland elements. One of the key taxa in this analysis is *Podocarpus*. Pollen grains of three different types of *Podocarpus* were recorded in all three lakes (Fig. 16). One type was relatively small ca. 50–60 μm , whereas another was 80–110 μm , and the third was much more elongated. It is probable that these palynomorphs represent three different species of *Podocarpus* growing on the inselberg. A single species of *Podocarpus*, *P. lambertii*, grows in lowland Amazonia, and while it is possible that one of our pollen types is from this species, a minimum of two pollen types belong to species apparently restricted to montane settings.

The closest documented modern *Podocarpus* population to the Hill of Six Lakes is on the Pico da Neblina a mountain rising to 3014 m, 90 km to the northeast. A survey of herbarium sheets was used to construct a table of the lowest occurrence of *Podocarpus* in the Pico da Neblina and northwestern

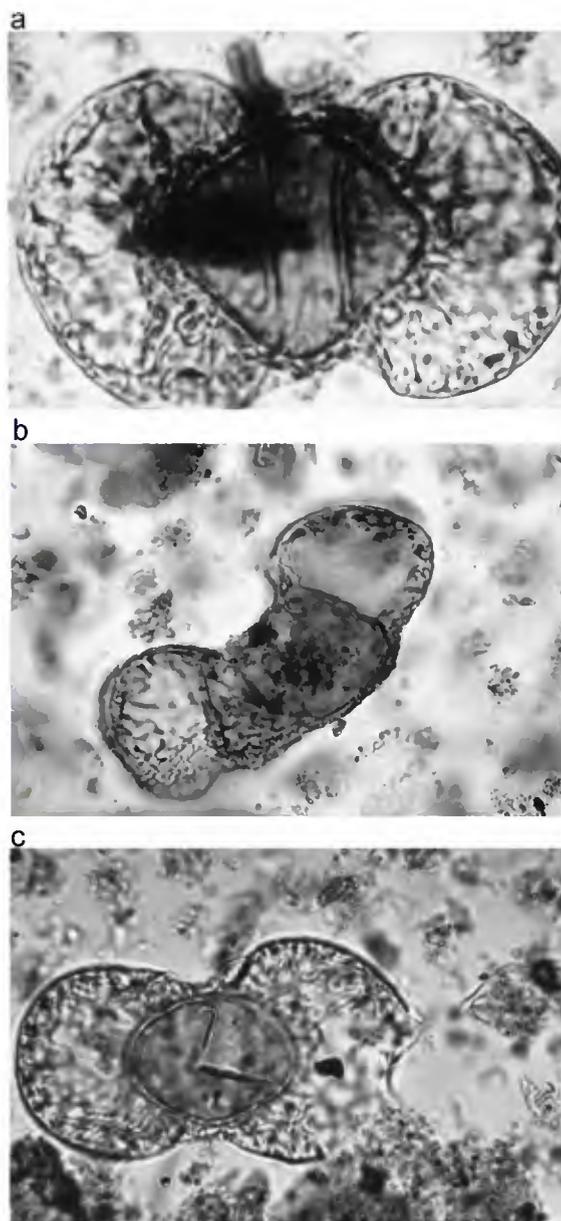


Fig. 16. Photomicrographs of three different types of fossil *Podocarpus* pollen recovered from lake sediments from Dragão and Pata, Brazil.

Amazonian uplands (Table 5). From this table it is evident that three species of *Podocarpus* could be found to co-occur at 1200 m elevation, about 900 m above the elevation of the Hill of Six Lakes.

Podocarpus pollen grains look somewhat like pine pollen but it should not be assumed that *Podocarpus*

Table 5

The lowest occurrence of *Podocarpus* species in northwestern Amazonia

Species	Elevation (m)
<i>P. bucholzii</i>	2100
<i>P. magnifolius</i>	1725
<i>P. roraimiae</i>	1200
<i>P. steyermarkii</i>	1200
<i>P. tepuiensis</i>	1100

Data from herbarium sheets at the Chicago Field Museum of Natural History and the New York Botanical Garden.

pollen is either as well-dispersed or as abundant as pine pollen. We have data from >300 modern pollen samples from Amazonia and Central America and have never had a single sample dominated by *Podocarpus* pollen in the way that *Pinus* dominates some temperate records. Even when pollen traps are set directly beneath *Podocarpus* trees only 20% *Podocarpus* pollen was recovered (Bush, 2000). When *Podocarpus* was locally abundant, but not directly overhead, <1% of *Podocarpus* pollen was found (Behling et al., 1997), and in >90% of lowland traps there was no *Podocarpus* whatsoever (Bush, 2000; Bush and Rivera, 1998). The inescapable conclusion is that for *Podocarpus* to be represented with 3–10%, as found in all three lakes, these trees were abundant in the local forest, and were probably growing within the watersheds of all the lakes. Other upland taxa that were found within these forests were *Weinmannia*, *Humiria*, *Ericaceae*, *Eugenia*, and *Myrsine*. These taxa are associated primarily with mid-elevation forests and are rare in modern lowland settings. *Alnus* pollen, though present, is not found in sufficient quantities to demonstrate its local occurrence.

Interestingly, *Ericaceae* and *Myrsine* are both present in the modern pollen rain of the Hill of Six Lakes, but there is no representation of *Podocarpus*, *Hedyosmum*, *Weinmannia* or *Alnus*. The lowland presence of taxa that are more often associated with upland conditions, e.g. *Hedyosmum* in western Amazonian swamps (Silman pers. comm.), *Weinmannia* in lowlands of the Chocó (J. Bradshaw pers. comm.) and *Myrsine* on the Hill of Six Lakes, could indicate that these taxa are not particularly stenothermic. Alternatively, it may be that these are relictual populations in the same way that boreal taxa can be found as remnants of widespread populations of the

past that now persist far from their ‘normal’ distribution in North America and Europe. Clearly, some caution is needed in interpreting the occurrence of individual taxa, but when a suite of upland species is found to have invaded a downslope location, evidence of climate change is robust.

This comparative study of the community histories in the three different watersheds, therefore, confirms the preliminary conclusion of the original report on Lake Pata that the arrival and disappearance of montane elements in the forests of the Lake Hill Plateau takes place against a backdrop of relative constancy (op. cit.). Taking the evidence for the migration of upland elements together, we infer that cold-loving elements expanded downslope and invaded the lowland forest. A descent of 800 m to 900 m would be sufficient to bring all these elements to the elevation of the Hill of Six Lakes. This would provide a minimum cooling of 4–5 °C assuming an adiabatic moist air lapse rate of ~5 °C (Bush et al., 2001; Colinvaux et al., 1997). The nearest uplands with modern populations of these species are about 90 km from the Hill of Six Lakes. However, the isolation of the inselberg from other upland areas makes it inherently unlikely that this hilltop would have been colonized by so many cold-adapted taxa if the intervening lowlands were not a seed source. If *Podocarpus* and the other taxa had invaded the bottomlands, rather than just the plateau of the inselberg, then a vegetation descent of 1000 to 1100 m is required, which translates to a temperature depression of 5–6 °C. This estimate of cooling is entirely consistent with other pollen data (Bush and Rivera, 2001; Bush et al., 1990; Colinvaux et al., 1997; Liu and Colinvaux, 1985) and with isotopic analyses of groundwater (Stute et al., 1995).

The arrival and disappearance of the montane elements in the pollen record takes place against a backdrop of relative constancy. Despite some taxonomic uncertainty, the forest that existed on the inselberg in the past appears broadly similar to that of the present. The combination of Melastomataceae/Combretaceae, Myrtaceae, *Alchornea/Aparisthemum*, and Moraceae/Urticaceae as the most common pollen types is the same in the Pleistocene and the Holocene. This observation raises the broader issue of whether lowland species could withstand the kind of climatic change inferred from the pollen record. Without an

elevational range of sites through which migrations can be tracked, no direct observation can be made regarding lowland species response to climate change. However, recent studies in Amazonian Peru and Ecuador provide insights into the potential resilience of community members to habitat change. [Terborgh and Andresen \(1998\)](#) demonstrated that there was considerable overlap of species, between terra firme and flood forest habitats. They determined that γ -diversity (sensu [Cody, 1975](#)) was a stronger predictor of differentiation in species lists than β -diversity (sensu [Whittaker, 1960](#)). [Pitman et al. \(1999\)](#) demonstrated that, contra earlier studies (e.g. [Gentry, 1989](#)), over large areas few species are truly habitat-specific. Less than 15% of species were found to be unique to a certain habitat type and that where there was turnover between habitats there was often a congeneric replacement of species ([Pitman et al., 1999](#)).

At the species level no evidence exists as to the temporal frequency with which community dominants turnover. Dominance was considered by many ecologists to be a feature of temperate rather than tropical forests, but a study by [Pitman et al. \(2001\)](#) documented that a predictable subset of the larger trees in a forest plot were much more abundant than randomness predicts. In a comparison of Peruvian and Ecuadorian terra firme forests on similar soil types, [Pitman et al. \(2001\)](#) found that a non-random group of species has the highest abundances at both sites. What makes the dominance of this oligarchy even more remarkable is that it occurs under markedly different climatic regimes. In Peru, the study site received 2300 mm precipitation with a 3–4-month dry season, while in Ecuador the forest received 3200 mm precipitation more or less evenly distributed through the year. Furthermore, the minimum temperatures recorded for these sites ranges from 4.5 °C for the upper elevations of this vegetation type at Manu to never less than 10 °C at Yasuni ([Pitman et al., 2001](#)). As the tolerable ranges in temperature (ca. 5.5 °C) and precipitation (ca. 35%) are similar to, or greater than, our inferred climatic change at the Hill of Six Lakes, it should be unsurprising to find that the most abundant plants of today were also abundant in the Pleistocene.

We hypothesize that the migrational response to Pleistocene climate change in tropical forests was essentially dissimilar to the long-range migrations

advocated for temperate systems (e.g. [Davis, 1981](#); [Huntley et al., 1989](#); [Webb, 1987](#)). In temperate regions, the scale of vegetation response was much greater than in the tropics, both in terms of the distance migrated and the chance of going locally extinct. The tropical floras of the Pleistocene were undoubtedly different to those of today, but ever since the first cooling of the lowland tropics was demonstrated there has been the persistent question “where did the species go?” We suggest that to a large extent the lowland taxa did not migrate, and those taxa that are common today may even have remained common in the past. These oligarch species comprise the essential fabric of the forest. The lesser floristic components that turnover spatially today, are probably those that were most affected by competition from the montane taxa and turned over temporally. Clearly, this hypothesis of a persistent oligarchy of species needs to be tested rigorously.

5.4. Could the vegetation of the Hill of Six Lakes have been caatinga not forest?

[Pennington et al. \(2000\)](#) argued that many of the pollen taxa documented by [Colinvaux et al. \(1996\)](#) in the Pata record could equally come from caatinga as from mesic forest. Of course, many taxa are shared between habitats, but [Pennington et al. \(2000\)](#) ignore the quantitative aspect of the pollen record and the wealth of modern pollen rain data from savanna and caatinga ([Bush, 2000](#); [Salgado-Labouriau, 1979](#); [Salgado-Labouriau, 1997](#); [Salgado-Labouriau et al., 1997](#)) and many types of mesic tropical forest ([Behling et al., 1997](#); [Bush, 1991](#); [Bush, 2000](#); [Bush and Rivera, 2001](#); [Bush and Rivera, 1998](#); [Grabandt, 1980](#); [Grabandt, 1985](#); [Rodgers and Horn, 1996](#); [Salomons, 1986](#)). In savanna systems Poaceae pollen often reach values of 50–90% ([Salgado-Labouriau et al., 1997ab](#)), and in open woodland settings Poaceae pollen is seldom <20%. [Berrio et al. \(2000\)](#) found that substantial fringes of riparian vegetation 2–3 km breadth could damp this savanna signal in a lake of 150 m diameter, so that Poaceae pollen only accounted for 20% despite the lake lying in a predominantly savanna habitat.

At the Hill of Six Lakes there was no gallery forest surrounding the lakes, as the lake basins drop abruptly from the terra firme surface. Even so, Poaceae rarely

exceeds 2%, and never exceeds 5% in samples from the Hill of Six Lakes. In habitats with incomplete canopy cover weedy species flourish. *Cecropia* is often abundant (20–30%) in such settings unless it is very dry (<1500 mm precipitation (Bush, 2002)). At the Hill of Six Lakes, *Cecropia* is consistently a minor component of the pollen rain.

In savannas and open woodlands the diversity of arboreal taxa is usually low because weedy, anemophilous species thrive and the pollen rain becomes dominated by one or a few taxa that produce vast amounts of pollen, e.g. *Cecropia*, *Bursera*, and *Trema*. In closed forest, the diversity of pollen types increases, with a greater proportion of relatively rare types. A consistent pattern in the Hill of Six Lakes records is that there is no such dominance by an over-represented taxon and there are consistently high arboreal diversities (see the list for pollen zone Pata-2, above). Just as in the Manu and Yasuni study, the broad description of the biome can be done using the most abundant species, but the habitat specific information lies in the rarer taxa. The lake sediments all contain *Cedrela*, *Cyathea*, *Podocarpus*, *Myrsine*, *Brosimum*-type (within *Urticaceae/Moraceae*), abundant and diverse ferns, taxa that are highly characteristic of closed mesic forest.

Lastly, in all the open vegetation types that we have investigated, fire is an important ecological component and it leaves a clear charcoal signature in the sedimentary record. Charcoal is rarely present in these samples and its occasional occurrences are consistent with rare natural fires as a result of lightning strikes. An increased abundance of charcoal in the Holocene is consistent with observations of increased fire frequency in the forests of San Carlos (Saldarriaga and West, 1986) ca. 100 km from the Hill of Six Lakes. Certainly the abundance of charcoal never attains the frequency of charcoal associated with savanna, cerrado, caatinga, or even seasonally deciduous forest (Kershaw et al., 1997; Salgado-Labouriau, 1979). Even during the time of no organic accumulation between 33,000 and 27,000 cal BP there is no concentration of charcoal. Charcoal does not oxidize and there is no apparent mechanism to prevent its accumulation. Therefore the lack of charcoal in this period, in all three records, is powerful evidence against establishment of dry forest conditions on the hill or the surrounding plains.

5.5. The Hill of Six Lakes, seasonality, and the Pleistocene landscape

That Pleistocene lake level rose and fell cyclically without a corresponding change in the vegetation may reflect changes in precipitation seasonality. During the wet season a massive surplus of water in the Amazonian system swells lakes and rivers. In northern Amazonia, wet season potential evapotranspiration (PET) is much smaller than water supply (Richards, 1996). As the duration of seasonal PET and soil moisture deficits are key determinants of vegetation types, wet season precipitation could be reduced substantially without influencing vegetation at the Hill of Six Lakes.

Pata, Dragão and Verde are effectively evaporation dishes with a leak. They require regular topping up to stay deep. The greater their leakiness the greater the input of water required. It is probable that wet season rains provide the majority of water stored in the lake and that dry season rains are generally sufficient to maintain lake level.

Given that the Hill of Six Lakes supports very thin soils the water holding capacity of these soils is small. As the modern vegetation already shows considerable edaphic modification compared with forests at the base of the hill, we may assume that this system would be unusually susceptible to a strengthening of the dry season. As we see no evidence of an increase in dry flora indicators, we infer that the dry season precipitation was not significantly reduced, but that the reduction in precipitation that caused lake low-stands occurred in the wet season.

These observations are entirely consistent with the seasonality that would be predicted based on the insolation. When JJA insolation peaks, DJF insolation is lowest. Consequently, convective activity is increased during the dry season and is reduced during the wet season, effectively reducing overall seasonality. In the opposing cycle where DJF insolation is highest, seasonality is accentuated. Even during these phases there is no evidence of increase of open ground species, or elevated concentrations of charcoal. A mesic forest was maintained throughout the last two glacial cycles. Indeed, a recent mineralogical study of Amazonian fan sediments (Kastner and Goni, 2003) reveals no significant differences in composition between glacial and interglacial sediments, bolstering

our observation that there were not widespread biome oscillations between forest and savanna at the Hill of Six Lakes during the late Quaternary.

Our data are consistent with a cyclic reduction in wet season rains reaching a nadir in the period from 35,000 to 26,000 cal. BP. Quantifying this change is not possible on the available data, but it should be noted that these edaphically dry settings would have been very susceptible to increased aridity, and yet they maintained a cover of diverse mesic forest taxa.

Compounding the difficulty of deducing paleoprecipitation from sparse records is the complicating factor of changes in the partial pressure of CO₂ (ca. 180 ppm at the LGM) that may have induced changes in plant distributions (e.g. [Street-Perrott et al., 1997](#)). The principal effect of reducing CO₂ availability will be to cause plants to have longer stomatal opening times and hence experience elevated drought stress. Thus lowered CO₂ will exacerbate any soil moisture deficit, but has much less effect if there is a plentiful supply of water.

Temperature also plays a role in the competitive relationship between C3 and C4 plants. Under present CO₂ concentrations the “crossover temperature”, i.e. temperatures below which the C4 pathway is competitively superior occurs at about 18 °C at 270 ppm CO₂ ([Ehleringer, 1997](#)). However, under 180 ppm atmospheric CO₂ this crossover point is at about 10 °C ([Boom et al., 2001](#)). Thus the combination of lowered temperatures and partial pressure of CO₂ should have favored C4 plants. Over portions of their range, C3 plants would be expected to be replaced by C4 plants. It is even argued that the replacement of trees with grasses in montane Africa may have owed more to lowered CO₂ concentration than temperature depression ([Jolly and Haxeltine, 1997](#)).

Models suggest that lowered LGM temperatures should have led to reduced evapotranspiration rates that may have offset much of this additional drought stress ([Cowling and Sykes, 1999](#)). C3 trees may have compensated for the reduced availability of CO₂ by reducing their leaf area index ([Cowling et al., 2001](#)). Competitive differences under each new climatic regime would bring about species turnover and a vegetation response as new morphological traits such as deciduousness, or more open canopy structure were favored. Such shifts in forest composition are entirely consistent with the palynological record. Perhaps it is

instructive to turn the CO₂ argument around and observe that *despite* lowered temperatures and lowered CO₂, the edaphically dry Hill of Six Lakes still maintained its forest cover. Therefore, aridity was not a sufficient factor to cause a turnover in biomes in this region of Amazonia.

In a region that receives >2000 mm of precipitation per annum, it is seasonality rather than total precipitation that sets biomes ([Bush et al., 2004](#); [Sternberg, 2001](#)). The wet season will generally have a large excess of water, much of which runs off, or is evaporated without ever entering biological systems. A reduction in wet season rain may reduce the excess water in the system, but would have to be very severe to affect forest composition. However, in the dry season, plants are much more vulnerable to even small fluctuations in precipitation or duration of droughts. Consequently, variation in wet season precipitation could significantly affect lake level without causing a parallel change in the forest, whereas a change in dry season precipitation is more likely to influence both lake level and forest composition. We suggest that the observed cyclic reduction in lake level observed at Lake Pata was the result of reduced wet season precipitation. The lack of apparent change in forest cover strongly suggests that in this edaphically dry landscape there was no significant reduction in dry season precipitation.

Pleistocene cooling, as documented from Ecuadorian Amazonia ([Bush et al., 1990](#); [Colinvaux et al., 1997](#); [Liu and Colinvaux, 1985](#)) and southeastern Amazonia ([Ledru, 1999](#); [Ledru et al., 2001](#)), not aridity, was the dominant effect on this landscape. The invasion of upland taxa into the lowlands was not a local event, but seems to have been widespread across the Amazon basin. In this wet continent, cold-tolerant trees prevailed and there is no evidence of significant expansions of C4 grasses within the northwestern Amazon basin.

6. Conclusions

These pollen data, independent evidence from groundwater ([Stute et al., 1995](#)), and a reappraisal of the sea-surface temperature data ([Mix et al., 1999](#)), lead to a reconstruction of a 5 to 6 °C cooling at the LGM in Amazonia ([Hostetler and Mix 1999](#)). However, as the ice records (e.g. [Dansgaard et al., 1993](#);

Thompson et al., 1998) and ocean records (e.g. Bond et al., 1993; Friedrich et al., 2001) have demonstrated, Pleistocene temperatures were far from constant. Cold events that permitted montane species to invade the Amazon lowlands may have been of short duration, lasting just a few thousand years. Equally, warm events (the Holocene being an extreme and protracted one) that forced an upslope range contraction of species were mostly brief events.

It is not possible to characterize the Pleistocene as “wet” or “dry”. Throughout the Pleistocene lake levels oscillated presumably due to changes in wet season precipitation, but within the last 170,000 years each of these events appears to have followed an orbital cycle with a 22,000 year periodicity. Consequently, the peak of each dry phase was a relatively brief period. If as we suggest the change in seasonality was a change in wet season precipitation, though lowering lake-levels this would not have a correspondingly large impact on forests. With so few paleoecological data from Amazonia it is best to wait before attempting to quantify past precipitation conditions. However, some qualitative observations can be made: The wettest episodes appear to have maintained lakes above their present stage, and the driest episodes were enough to cause shallow lakes to become ephemeral. However, only one of eight documented cycles appears to have been of sufficient intensity to cause a 3-m-deep lake to become ephemeral. In this phase, lake depth was reduced sufficiently to allow oxygenated water to lie at the mud–water interface, but the difference between inflow, leakage and evaporative loss was not sufficient to cause this water body to dry out completely. There does not appear to be uniformity in the timing of low lake stand events (contra Ledru et al., 1998) across Amazonia as climate change was temporally and spatially heterogeneous.

No evidence is found of a change in biomes at the Hill of Six lakes in the last 170,000 years. Intact forest is evident at all three sites, despite fluctuating lake levels. The most parsimonious explanation of the data is that cooling reduced wet season convective activity, thereby reducing overall precipitation and lake level. However, forests in this section of Amazonia are relatively resistant to changes in wet season rains, but would be much more susceptible to changes in dry season precipitation. As no evidence is found to suggest increased forest openness, we infer that dry season precipitation was largely unchanged.

From the available records it is evident that the Pleistocene of South America was a period of intense and rapid climate change (e.g. Baker et al., 2001; Betancourt et al., 2000; Hooghiemstra et al., 1993; Thompson et al., 2000; van der Hammen and González, 1960). However, much has yet to be resolved regarding the response of South and Central American systems to orbital forcing. Some records suggest a strong concurrence with Milankovitch cycles (Harris and Mix, 1999; Hooghiemstra et al., 1993; Leyden et al., 1994), while others do not (Heusser et al., 1999). Although we find a strong orbital signal in lake chemistry, no equivalent change in vegetation is detected. Indeed, the principal conclusion that is reached from this study is that despite changes in plant community composition in response to cooling, the biome characteristic remained unchanged throughout. These records provide a unique, replicated, overview of community change, and biome stability for the lowland neotropics across a glacial cycle.

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