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SPECIAL ISSUE

A regional study of Holocene climate change and human occupation in Peruvian Amazonia

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ABSTRACT

Aim To investigate the influence of Holocene climatic and human-induced changes on a region of high biodiversity in southern Peruvian Amazonia.

Location Four palaeoecological records from separate lakes within a lake district close to the modern city of Puerto Maldonado, Peru.

Results The lakes provide a palaeoecological record spanning the last 8200 years. A mid-Holocene dry event is documented in all of the records that extend back > 6000 years. The dry event appears to have lasted from *c.* 7200 yr BP until *c.* 3300 yr BP. The onset of wetter conditions coincides with the formation of the youngest of the four lakes. The earliest occupation of these sites is inferred from the presence of charcoal at 7200 yr BP, and the first crop pollen is found at 3630 yr BP. Lakes that were regularly occupied were colonized soon after they formed. A reduction in charcoal concentration and the absence of crop pollen after *c.* 500 BP in all lakes is consistent with site abandonment following conquest.

Main conclusions The mid-Holocene dry event is suggested to be part of a time-transgressive drying that tracked from north to south in both the Andes and the Amazon lowlands. The last millennium may represent the period of highest sustained lake levels within the Holocene. The proximity of the four lakes allows a landscape-scale analysis of the spatial extent of human disturbance centred on a known site of human occupation and reveals the highly localized nature of pre-Columbian anthropogenic disturbance in Amazonian landscapes. Inferences regarding widespread pre-Columbian landscape modification by indigenous peoples must take into account key site attributes, such as seasonality and proximity to rivers.

Keywords
Amazonia, aridity, charcoal, drought, fossil pollen, human disturbance, Holocene, maize, manioc, rain forest.

INTRODUCTION

Most palaeoecological research has focused on glacial–interglacial oscillations as the major climatic changes in Amazonia during the Quaternary (Haffer, 1969; Colinvaux *et al.*, 2000; Pennington *et al.*, 2000). Nevertheless accumulating data point to the importance of Holocene cycles of drought as a potent force shaping lowland communities. Servant *et al.* (1981) predicted the presence of a mid-Holocene arid phase in Amazonia based on geomorphological evidence from Bolivia. This prediction has been borne out by subsequent palynological evidence of drought in such environmentally sensitive locations as the Bolivian savanna/forest ecotone (Mayle *et al.*, 2000), the Carajas Plateau, Brazil (Absy *et al.*, 1991) and the Colombian Llanos (Behling, 1998; Behling & Hooghiemstra, 1999). However, the timing of these events differs between localities, and it should be noted that no evidence of an equally strong mid-Holocene drying is evident in central Amazonia (Bush *et al.*, 2000; De Toledo, 2004).

While many sites within Amazonia reveal pronounced Holocene climate change, the probability of those changes strongly influencing vegetation structure is enhanced in the ecotonal areas between savanna and forest biomes. The origin of these climatic changes has variously been ascribed to orbital variation (Rowe *et al.*, 2002), El Niño/Southern Oscillation

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(ENSO; Moy *et al.*, 2002) and migration of the Intertropical Convergence Zone (Haug *et al.*, 2003).

The Holocene has also been the time of population and agricultural expansion in Amazonia. The Amazon lowlands have been occupied by humans for at least the last 11,000 years (Roosevelt *et al.*, 1996), and coastal agriculture was being practised in coastal Ecuador as early as *c.* 10,000 calibrated yr BP (hereafter all dates are expressed in calibrated years as cal yr BP) (Piperno & Stothert, 2003). In Amazonia, ceramics were used by *c.* 7000 cal yr BP (Roosevelt *et al.*, 1991) and maize agriculture had been adopted by 6000 cal yr BP (Bush *et al.*, 1989). By the time of European contact, Denevan (1976) estimated the indigenous human population of Amazonia to have been between 5 and 10 million.

The scale of Pre-Conquest human-induced landscape change remains controversial. Some have argued for dense settlements and extensive landscape conversion to create 'parkland' (Erickson, 2000, 2001; Heckenberger *et al.*, 2003; Stokstad, 2003) while others have maintained that existing data are consistent with lesser scales of land use and relatively sparse occupation (Denevan, 1996, 2003; Meggers, 2003).

Palaeoecology provides a tool with which to test hypotheses of climatic and human impacts on systems, and, as in all science, support for different causal explanations of observed changes is strengthened by analysis of replicates. Most palaeoecological studies of Amazonia have previously been based on isolated sites, or 'neighbouring' sites that lie 50–100 km apart (Bush *et al.*, 2000; Mayle *et al.*, 2000). Here, we describe palaeoecological records from four lakes that lie close together (three within 25 km of one another and a fourth within 50 km) in a lake district in southern Peru. These data provide the first landscape-scale view of changes in Holocene Amazonia and include both climatic and anthropogenic signals.

METHODS

Study area

A lake district containing *c.* 50 lakes and swampy depressions in a matrix of coarse white quartz sands lies on a nearly flat, little-dissected peneplain to the north of Puerto Maldonado, Peru (Table 1). The origin of the lakes is unknown, but they lie at the highest points on the rolling landscape well outside of fluvial influence (Fig. 1).

The four lakes used in this study were previously unnamed, and we have named them for botanists of the region. The lakes lacked inflowing streams, and their permanence was indicated by the presence of fish. The lakes appeared to be mesotrophic and were fringed by beds of emergent aquatics including *Sagittaria*, *Pontederia* and *Eichornia*.

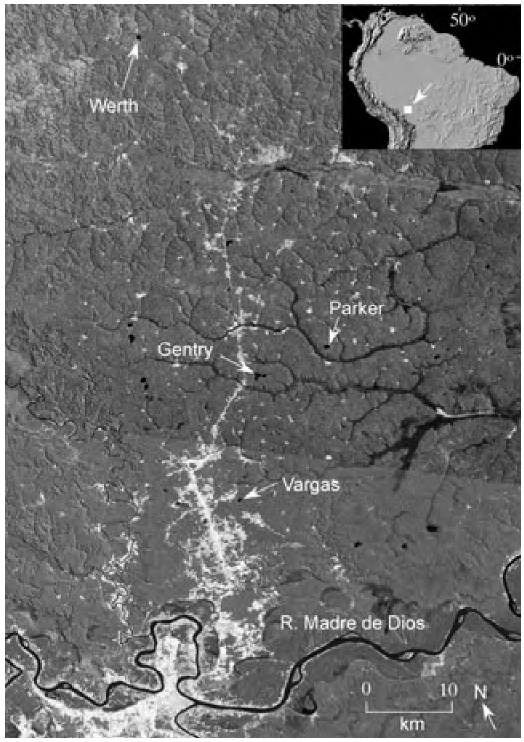

Figure 1 Annotated satellite image of the Puerto Maldonado lake district, Peru, showing the relative location of lakes Gentry, Parker, Vargas and Werth. The inset map shows location within South America.

The forests in south-eastern Peru have been extensively studied (Foster, 1990; Gentry, 1990; Terborgh *et al.*, 1996; Pitman *et al.*, 1999, 2001; Phillips *et al.*, 2003; Masse, 2005). Out of *c.* 600 individual trees ≥ 10 cm d.b.h. per hectare typically found in the semi-deciduous rain forest on Pliocene alluvium, *c.* 170 species are represented (Pitman *et al.*, 2001). In terms of number of species, the overstorey is dominated by (in descending order) Fabaceae, Lauraceae, Moraceae, Annonaceae, Sapotaceae and Euphorbiaceae (Pitman *et al.*, 2001). In terms of numbers of stems, the dominants become Arecaceae, Moraceae, Fabaceae, Malvaceae and Violaceae (Masse, 2005) with an understorey comprising saplings of canopy trees, treelets (particularly in the Monimiaceae and Violaceae;

Table 1 Basic geographical attributes of lakes Parker, Gentry, Vargas and Werth in Peruvian Amazonia. Data, apart from water depth, from Google Earth.

Lake	Latitude/longitude	Water depth (m)	Elevation (m)	Size (m)	Distance from nearest river (km)
Parker	12°08′31″S/69°01′15″W	2	289	650 × 500	29
Gentry	12°19′57″S/68°52′28″W	3	270	700 × 500	20
Vargas	12°20′03″S/69°07′04″W	2	246	1100 × 800	13
Werth	11°44′43″S/69°14′02″W	1.5	302	500 × 500	32

Phillips *et al.*, 2003), understorey palms and scattered patches of the bamboo *Guadua* spp. Around lakes there is an increased abundance of wetland-tolerant and other light-demanding taxa, e.g. Cecropiaceae, Fabaceae, *Mauritia flexuosa* (Arecaceae), Heliconiaceae and grasses.

The lake district is distinct from the broader expanse of forests in south-east Peru in being unusually rich in Lecythidaceae, particularly *Bertholletia excelsa* and *Couratari* spp. (Masse, 2005). The nuts of *B. excelsa* are commercially harvested in the region. Apart from the increased abundance of certain Lecythidaceae, the forests are similar in character and composition to the others described for the region (e.g. Pitman *et al.*, 2001; Phillips *et al.*, 2003; Silman *et al.*, 2006).

The lake district lies across a region of sharply changing precipitation with *c.* 2000 mm yr^{-1} in the south compared with *c.* 1700 m yr^{-1} in the north. A similar gradient exists in length of the dry season, ranging from 2 months' duration in the south to 4 months in the north. A large Indian midden rich in pottery lies beside the road within 1 km of Lake Gentry.

Field and laboratory techniques

Between 1999 and 2001, cores were raised from the centre of each lake using a Colinvaux–Vohnout coring rig from a raft of rubber boats. Cores were returned to the Florida Institute of Technology where they were opened, described and subsampled. Pollen analysis followed standard protocols (Stockmarr, 1971; Faegri & Iversen, 1989), and samples were counted at ×400–×1000 on a Zeiss Axioskop photomicroscope. Pollen identification was based on our pollen reference collection of > 3000 types and published descriptions (Roubik & Moreno, 1991; Colinvaux *et al.*, 1999). Pollen analysis was conducted by M.B.B. (lakes Vargas and Parker) and C.M.C.S.L. (lakes Werth and Gentry). A total of 300 terrestrial pollen types were counted in each sample, and a total of more than 450 pollen types were noted. Cyperaceae, Poaceae, other swamp taxa and spores, were excluded from the terrestrial pollen sum (their percentages are expressed as a proportion of terrestrial pollen). To search for rare grains of maize and manioc pollen, both of which are > 80 μm in diameter, processed residues of 1 cm^3 subsamples were filtered at 50 μm to remove fine material, mounted onto multiple slides and scanned at ×200. All Poaceae pollen grains accepted as maize had a distinctive surface pattern and a diameter > 80 μm.

Charcoal samples were disaggregated in 10% KOH and sieved with a 180-μm screen. Particles retained on the screen were recorded digitally and their area calculated through video-capture and analysis using NIH-image (Clark & Hussey, 1996; Clark & Patterson, 1997). Loss-on-ignition was conducted at 550 and 1000°C. Diatom analysis was attempted on these sediments but downcore dissolution of silica meant that only the upper 20 cm of each core contained well-preserved diatom assemblages. Diagrams were plotted using C2 (Steve Juggins, University of Newcastle).

Ordination of the data for each lake was conducted using versions of detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) in PC_ORD4 (McCune & Mefford, 1999). Ordinations were run using percentile fossil pollen data. Data sets were reduced to the 40 most abundant taxa for analyses of individual lakes. For the comparative analysis of the lakes, all fossil pollen data were combined into a single matrix. In this analysis all the aquatic taxa were excluded from the data set. As two different pollen analysts had generated the data, the data set was reduced to 21 common and distinctive pollen types (these generally accounted for > 80% of the dry land pollen).

RESULTS

Stratigraphy

The lake sediments were primarily composed of black gyttja rich in well-humified organics. The major differences were in the depth of an organic-rich layer that was 50 cm thick in Parker and Gentry but only 10 cm thick at Vargas. Werth lacked a distinct peat layer but its gyttja was increasingly rich in coarse organic debris toward the surface. The bottom of all cores ended in coarse white sands with a limey-clay matrix.

Chronology

Accelerator mass spectroscopy (AMS) ^{14}C ages were obtained for samples of bulk sediment in most instances. Macrofossils of terrestrial origin, e.g. sedge nutlets, or leaves were used where possible; however, some core sections contained few large fragments.

All of the lakes showed uneven rates of sediment accretion suggesting periods of little accumulation. Despite this unevenness there were few reversals in the AMS data, and where they occurred one date was a clear outlier (Table 2 & Fig. 2). Three dates, one each on Vargas, Gentry and Werth, were rejected as having modern contamination. The basal date for Werth of 15,100 cal yr BP was also rejected as this was almost certainly the pre-lake soil surface and contains an unknown amount of bioturbated material.

Ordinations

The DCA and NMDS ordinations produced very similar outputs. In all instances stress test scores were rather high, suggesting weak results in the NMDS analysis of individual sites; the DCA results are presented. R^2 values (Euclidean distance, McCune & Grace, 2002), for Axis 1 of each ordination were generally > 50%, with the junior axes generally explaining < 10% of the remaining variance.

Description of pollen zones

Lake Vargas

A record in which sedimentation begins at *c.* 7900 cal yr BP, but contains a depositional hiatus between *c.* 7200 and 1500 cal yr BP. The ordination results (Fig. 3) indicate that the

Table 2 Accelerator mass spectrometry (AMS) ^{14}C ages for samples from lakes Vargas, Parker, Gentry and Werth with calibrated ages using a Southern Hemispheric correction according to CALIB 5.0.1 (http://radiocarbon.pa.qub.ac.uk/calib/).

Lab number	Sample name	Depth (cm)	Fraction dated	d13C (‰)	14C age	Calibrated years BP	Median probable age
Vargas							
OS-38418	Vargas	55	Sediment	−27.2	> Modern	–	0
OS-38419	Vargas	80	Macrofossil	−29.86	945 ± 30	760-900	840
OS-39955	Vargas	88	Sediment	−28.74	1390 ± 30	1190-1300	1280
OS-39954	Vargas	110	Sediment	−28.53	6300 ± 45	7030-7250	7200
OS-35343	Vargas	166	Sediment	−24.43	7060 ± 60	7760-7930	7830
Parker							
		50	Macrofossil	−25	525 ± 25	510-530	520
CAMS 109894	Parker	110	Macrofossil	−25	2815 ± 35	2790-2920	2830
OS-38416	Parker	130	Macrofossil	−22.61	3530 ± 35	3690-3830	3750
CAMS 109895	Parker	167	Macrofossil	−25	5850 ± 35	6550-6660	6600
OS-38417	Parker	178	Macrofossil	−26.07	6140 ± 45	6810-7140	6950
OS-35829	Parker	216	Macrofossil	−27.11	6410 ± 45	7180-7410	7290
Gentry							
NSRL-11997	Gentry	33	a/b/a Macrofossil	−22.35	> Modern	–	0
NSRL-11998	Gentry	43	a/b/a Sediment	−25.06	940 ± 40	740-900	770
NSRL-11999	Gentry	49	a/b/a Sediment	−23.48	2250 ± 30	2150-2300	2270
	Gentry	51	a/b/a Sediment		2610 ± 50	2500-2750	2620
NSRL-12000	Gentry	77	a/b/a Sediment	−24.33	4070 ± 35	4430-4520	4490
	Gentry	106	a/b/a Sediment		5440 ± 40	6030-6280	6230
Werth							
CAMS-74839	Werth	37	a/b/a 0.08mg C	−25	580 ± 70	510-630	540
CAMS-75227	Werth	37	Humic	−27	1020 ± 50	800-930	840
NSRL-11994	Werth	50	a/b/a Sediment	−14.94	1070 ± 35	910-960	940
CAMS-75228	Werth	57	Humic	−27	1470 ± 40	1290-1350	1320
CAMS-74982	Werth	57	a/b/a Sediment	−25	1850 ± 40	1630-1810	1750
	Werth	90	a/b/a Sediment		3200 ± 45	3270-3440	3370
NSRL-11995	Werth	100	a/b/a Sediment	−18.93	130 ± 35	0-250	140
NSRL-11996	Werth	140	a/b/a Sediment	−23.19	12,750 ± 65	14930-15180	15100

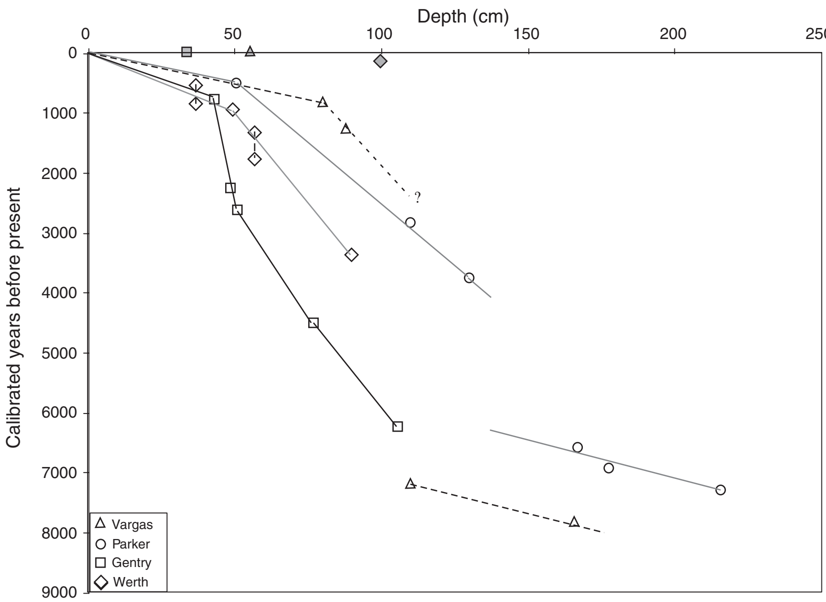

Figure 2 Depth–age plot of calibrated ages for radiocarbon dates from lakes Gentry, Parker, Vargas and Werth. Outliers are shown as filled symbols.

fossil pollen composition of all samples from within this core are broadly similar with the exception of the three basal samples.

Local Pollen zones V-1 (180–157 cm, 7900–7700 cal yr BP). Pollen concentration increased from close to zero at 190 cm (not shown), to *c.* 10,000 grains cm^{-3} at 170 cm (Fig. 4). This

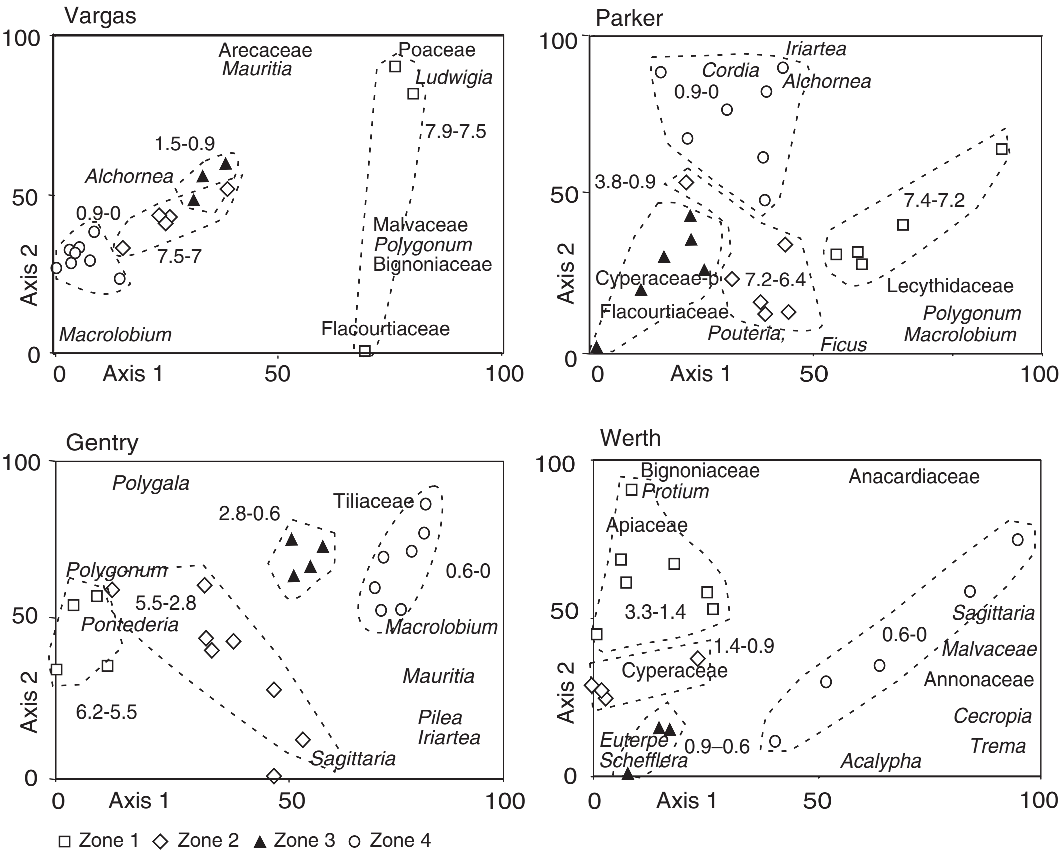

Figure 3 Results of the ordination of fossil pollen data using detrended correspondence analysis. Lakes were analysed separately using the 40 commonest pollen taxa in each record (including aquatics). In the following, numbers in parentheses are (eigenvalue, % variance explained): Vargas Axis 1 (0.366, 0.617), Axis 2 (0.051,0.028); Parker Axis 1 (0.234, 0.593), Axis 2 (0.077, 0.085); Gentry Axis 1 (0.395, 0.246), Axis 2 (0.102, 0.048); Werth Axis 1 (0.305, 0.791), Axis 2 (0.058, −0.015).

pattern matched a progressive change in sediment from sandy clay with low organic content to a clay-rich gyttja with 20% carbon. Poaceae (320%), Cyperaceae and other swamp elements dominated the pollen spectrum. However, the terrestrial pollen was rich in forest elements, e.g. *Schefflera* (ex *Didymopanax;* Araliaceae), Bignoniaceae, Urticaceae/Moraceae, *Cecropia* (Cecropiaceae), other arboreal pollen included Annonaceae, Lecythidaceae, *Luehea* (Tiliaceae), Meliaceae, *Pouteria* (Sapotaceae), *Picramnia* (Simaroubaceae), *Pseudobombax* (Bombacaceae), *Tetragastris* (Burseraceae), *Virola* (Myristicaceae) and *Zanthoxylum* (Rutaceae). Trilete spores were abundant at *c.* 35% of the terrestrial pollen sum. *Pontederia* increases in abundance in the uppermost sample to *c.* 40%. Despite the abundance of Poaceae in this zone no charcoal was present.

V-2 (157–110 cm, 7700–7200 cal yr BP). Pollen concentration increases to its peak of 70,000 grains cm^{-3} at the top of this zone. The sedimentary carbon content oscillates between *c.* 40% and 70% while terrestrial taxa are relatively constant in their representation. Urticaceae/Moraceae (comprising at least six pollen types) are *c.* 50% throughout this zone. The abundance of Pontederiaceae pollen is markedly higher than in the previous zone, and stable at *c.* 70%. Poaceae decline to generally < 50%, attaining a local nadir of *c.* 20% at 120 cm. Two samples contained a trace amount of charcoal in this zone.

V-3 (109–67 cm, *c.* 2540–800 cal yr BP). The onset of this period is uncertain. If the rate of sedimentation between the two ages at 80 cm and 88 cm depth is extrapolated downward, the base of this zone would be formed at *c.* 2540 yr BP. Pollen concentration is *c.* 30,000 grains cm^{-3} and the shape of this curve is mirrored in Cyperaceae abundance. Pontederiaceae falls steadily from 60% at the base of the zone to 30% at the top, while Alismataceae are consistently abundant at *c.* 20%. Poaceae pollen representation is higher than at the end of the previous zone, at *c.* 50%. Despite these fluctuations in the wetland pollen taxa, the terrestrial pollen representation is very similar to that of the preceding zones. Charcoal is present in the sample at 900 yr BP in concentrations suggesting a local fire. Two other minor peaks of charcoal, at the base and the top of the zone, were also recorded.

V-4 (67–0 cm, *c.* 800–0 cal yr BP). Sediment organic content is stable at *c.* 90% and pollen concentrations were low ranging between 5000 and 10,000 grains cm^{-3}. Pollen of wetland plants is generally scarce, with the exception of a spike of *Pontederia* representation (83%) in a single sample at the base of this zone. With the exception of the increase of the western Amazonian dominant *Iriartea* (Arecaceae) (18%), representations of arboreal taxa are broadly similar to those of the preceding zone.

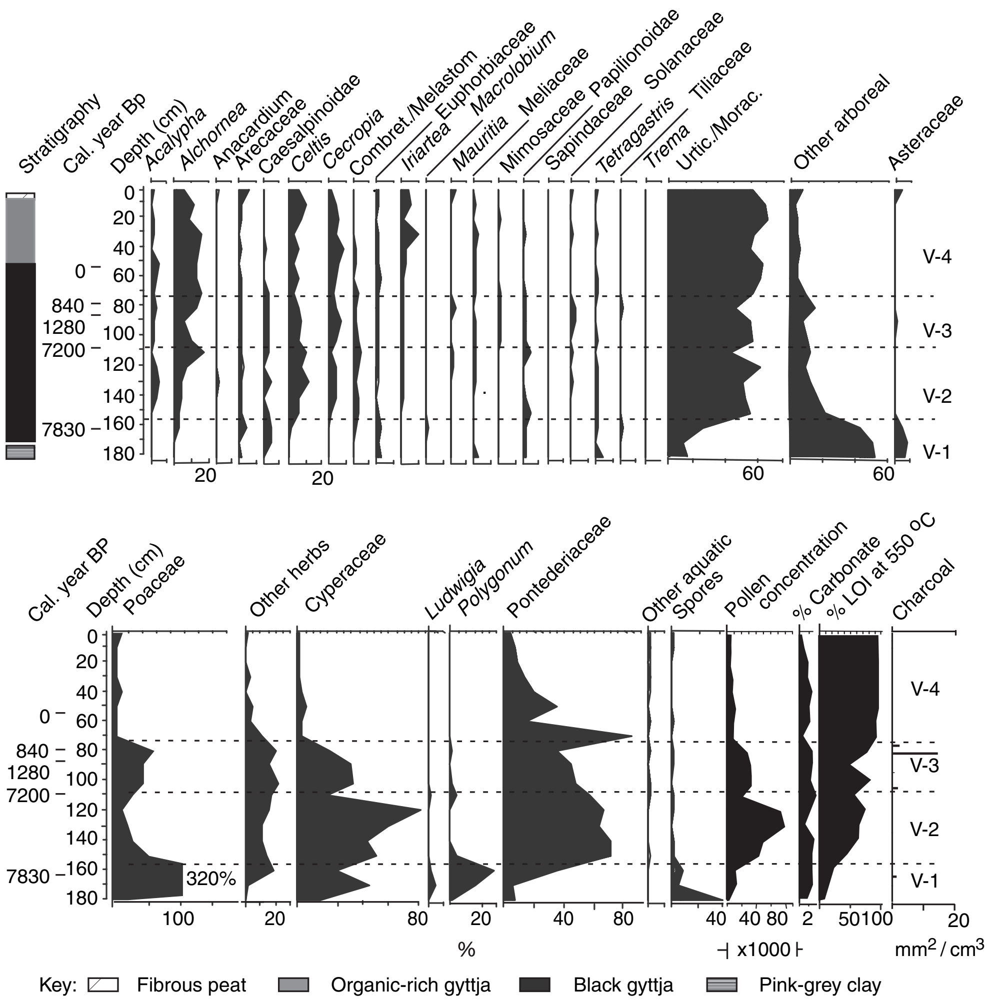

Figure 4 Percentage pollen diagram of selected taxa from Lake Vargas, Peru. Also shown are sediment stratigraphy, calibrated ages, loss-on-ignition results and charcoal and pollen concentrations.

Lake Parker

A lake that formed *c.* 7400 cal yr BP, but did not retain sediment between *c.* 6200 and 3800 cal yr BP. The basal zone of this record contains a substantial proportion of the total variability, and samples from the other zones in the core all have overlapping scores on Axis 1 of the DCA.

Local pollen zones P-1 (240–203 cm, *c.* 7400–7100 cal yr BP). Clay-rich sediments with *c.* 12% carbon content transition to organic-rich gyttja with *c.* 50% carbon at the top of the zone (Fig. 5). Pollen concentrations in the basal sample were 13,000 grains cm^{-3}, with the sample containing many broken and damaged grains. In other samples in this zone pollen concentrations exceeded 100,000 grains cm^{-3}. Pollen of Poaceae (190%), trilete spores, Cyperaceae (358%) and other swamp elements were abundant. A distinctive pollen type that we tentatively identify as a type of Cyperaceae (Cyperaceae-b) was found in this core and in that of Gentry. We are confident that this is a herbaceous monocotyledonous type, similar to Cyperaceae. *Mauritia* (Arecaceae), *Macrolobium* (Fabaceae) and Cyperaceae-b are all associated with swamp forest, and the forest pollen spectrum is diverse. The proportion of Urticaceae/Moraceae pollen increases from 0% at the base of the zone to > 20% at the top of the zone. Charcoal is absent in the basal sample of the zone, but is present as early as 7200 cal yr BP. Thereafter charcoal is present in almost every sample throughout this core.

P-2 (202–135 cm, *c.* 7100–6200 cal yr BP). At the base of this zone the organic content of the sediment rises to > 95%. Pollen concentrations are high, with all samples having > 70,000 grains cm^{-3}. Poaceae pollen and all swamp elements decline in abundance at the start of this zone. The lowest Poaceae percentage of the entire core occurs at 170 cm, coinciding with extremely low values for Cyperaceae-a and a dip in organic carbon content to about 80%. Urticaceae/Moraceae pollen are abundant at *c.* 40–50% in most samples, and pollen of typical lowland forest elements, e.g. *Cecropia*, *Alchornea* (Euphorbiaceae), *Celtis* (Ulmaceae) and Papilionoid legumes, is more abundant than in the preceding zone. Charcoal is consistently present throughout this zone.

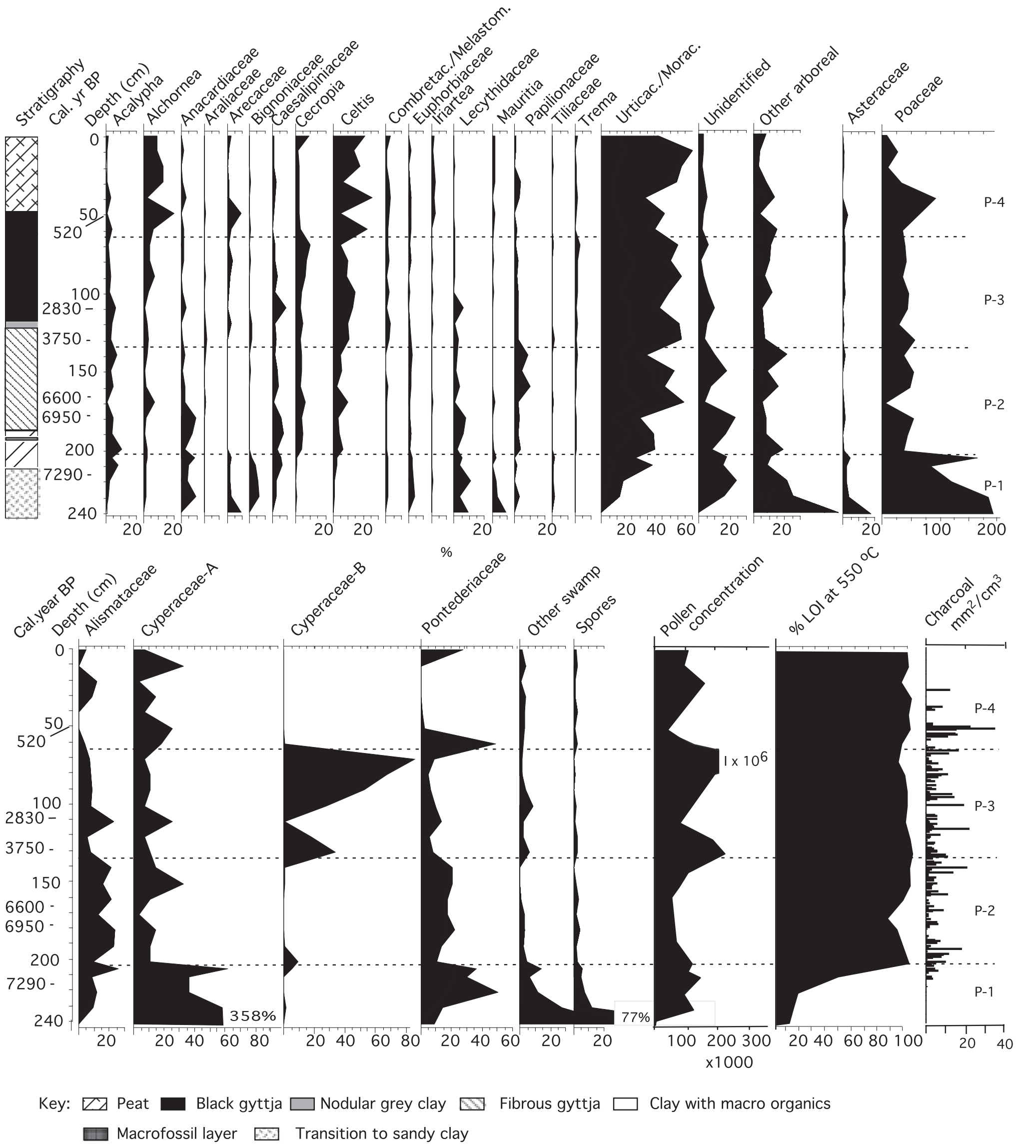

Figure 5 Percentage pollen diagram of selected taxa from Lake Parker, Peru. Also shown are sediment stratigraphy, calibrated ages, loss-on-ignition results and charcoal and pollen concentrations.

P-3 (134–65 cm, *c.* 4100–600 cal yr BP). Sediments of this zone exhibit a uniformly high, > 95%, carbon content and pollen concentration reaches its peak within the core with *c.* 1,000,000 grains cm^{-3}. The peak of concentration at 70 cm depth matches a peak of Cyperaceae-b pollen representation equivalent to 100% of the pollen sum. Other lake margin taxa, e.g. Pontederiaceae, Alismataceae and Cyperaceae-a, are also abundant in this zone. Charcoal is slightly more abundant in this zone than in P-2, and is not correlated with pollen concentration, suggesting that charcoal abundance and sedimentation rate are not tightly linked.

P-4 (65–0 cm, 600–0 cal yr BP). Sediment organic content is constantly high throughout this zone, and concentrations fall back to about 100,000 grains cm^{-3}. At 50 cm there is an abrupt change in composition from a humified organic gyttja to a red-brown fibrous peat. Pollen shows a transition across this boundary of increasing representation of *Alchornea*, *Celtis* and *Iriartea*, and a little later Urticaceae/Moraceae. Pontederiaceae and other swamp elements increase in abundance at the base of the zone, fall as Poaceae peaks at 40 cm, and then rise once more near the top of the zone. The highest peak of charcoal in this core is observed at *c.* 500 BP, followed by a decline and its longest absence at any time within the record in the last 250 years. The occurrence of charcoal becomes erratic in this zone before completely disappearing from the record at *c.* 250 cal yr BP.

Lake Gentry

The lake formed around 6200 cal yr BP and probably provides a more or less continuous sedimentary record between *c.* 5000 cal

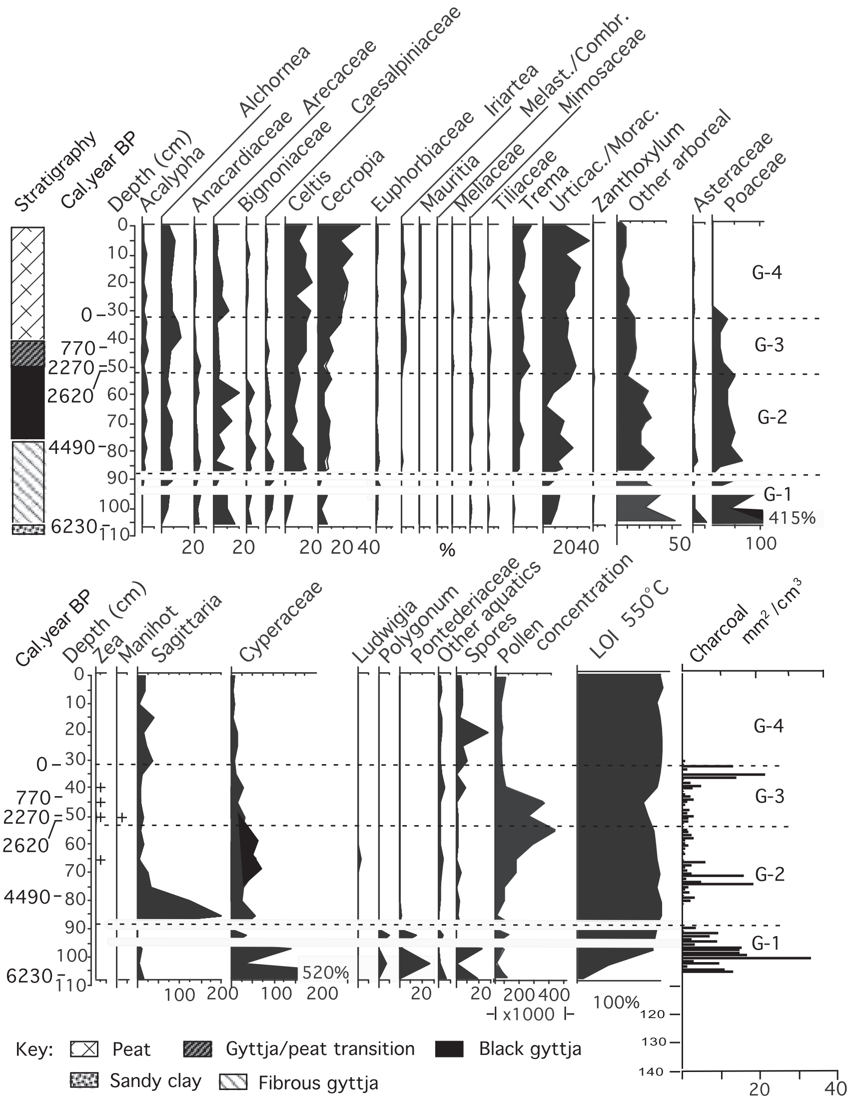

Figure 6 Percentage pollen diagram of selected taxa from Lake Gentry, Peru. Also shown are sediment stratigraphy, calibrated ages, loss-on-ignition results and charcoal and pollen concentrations.

yr BP and the present. Sample scores from the DCA provide strong statistical separation of the zones, with the most modern zone appearing to be well differentiated from earlier ones.

Zone G-1 (110–88 cm, *c.* 6200–?6000 cal yr BP). A low organic content and pollen concentration in the basal samples corresponds with the highest percentages of Poaceae (> 400%), Cyperaceae (> 500%) and Pontederiaceae in the core (Fig. 6). Two levels counted within this zone at 90 and 95 cm depth contained almost no pollen, whereas samples at 92 and 95 cm yielded pollen concentrations of 78,000 and 115,000 grains cm^{-3}, respectively. A diverse arboreal rain forest flora is evident, although values of Urticaceae/Moraceae (< 10%) are relatively low and the proportion of broken and unidentified tricolporate grains is relatively high. Charcoal was not found in the basal samples (110–106 cm), nor in the 30 cm of clay beneath this zone. At 105 cm the abundance of charcoal rises significantly, with concentrations greater than the highest amounts recorded at any of the other lakes.

Zone G-2 (87–52 cm, *c.* 5600–2800 cal yr BP). Pollen concentrations rise steadily throughout this zone from about 110,000 to 500,000 grains cm^{-3}. Subtle distinctions are evident in the gyttja of this zone, with the gyttja of the middle of the zone having the fewest plant macrofossils. The fibrous gyttja at the base of the zone corresponds with the occurrence of a peak of Alismataceae pollen (200%). The pollen spectrum of this peaty section is markedly different from that of the upper sample of G-1. Charcoal is absent at the base of this zone, but is found in almost all samples above 80 cm depth. Pollen of the cultivar *Zea mays* is found at 65 cm depth, *c.* 3630 cal yr BP.

Zone G-3 (52–32 cm, *c.* 2800–600 cal yr BP). This zone is transitional in terms of its sediment type with gyttja at the base, overlain by increasingly organic muds, and capped by a red-brown peat. Sedimentation is so slow that a hiatus is suspected within this zone. Pollen concentrations fall from *c.* 400,000 to 80,000 grains cm^{-3} at the transition to peat. The zone is marked by an increasing abundance of arboreal pollen taxa, e.g. *Alchornea*, *Cecropia*, *Celtis*, *Iriartea*, *Trema* and Urticaceae/Moraceae, while swamp elements continue to decline in abundance. Evidence of agriculture is strong with the occurrence of *Zea* and *Manihot* and regular occurrence of charcoal. In the uppermost section of the zone, within the peat, there are very high concentrations of charcoal, but no cultivars were found in those samples.

Zone G-4 (32–0 cm, *c.* 600–0 cal yr BP). Coarse red-brown peat with low pollen concentrations of *c.* 50,000 grains cm^{-3} characterize this zone. *Cecropia*, *Mauritia*, other Arecaceae and Urticaceae/Moraceae increase in abundance while Poaceae disappears from the record. Most swamp elements are scarce, although Alismataceae becomes more abundant than in the preceding zone. Charcoal is present in trace amounts in the basal sample of this zone, but thereafter is absent. Cultivars were not recorded in this zone.

Lake Werth

This lake formed about 3300 yr BP and appears to hold a continuous sedimentary record. The most recent zone is the only one isolated on DCA Axis 1, although the other zones are separated on Axis 2.

Zone W-1 (90–57 cm, *c.* 3300–1400 cal yr BP). This transitional zone is formed by a clay with a low organic content merging upward with organic-rich gyttja (Fig. 7). Similarly, pollen concentrations increase upward from 25,000 to 100,000 cm^{-3}. Pollen of Poaceae (> 50%), Cyperaceae and Alismataceae were abundant and arboreal elements were diverse with Urticaceae/Moraceae (*c.* 40%), *Celtis*, Bignoniaceae, *Cecropia* and *Mauritia* all evident. No charcoal was found in this zone.

Zone W-2 (67–37 cm, *c.* 1400–800 cal yr BP). Organic-rich gyttja with the highest pollen concentrations (*c.* 200,000 grains cm^{-3}) of the core are found at the base of this zone. Poaceae pollen increases to *c.* 100% and Cyperaceae maintain values of 15–30%. Urticaceae/Moraceae pollen reach a maximum abundance at 40 cm depth, immediately overlain by sediment that yielded the only occurrence, three very small fragments, of charcoal in this core.

Zone W-3 (37–22 cm, *c.* 800–400 cal yr BP). A marked increase in carbon content is evident in this section of the core, though core colour is unchanged, and the transition from

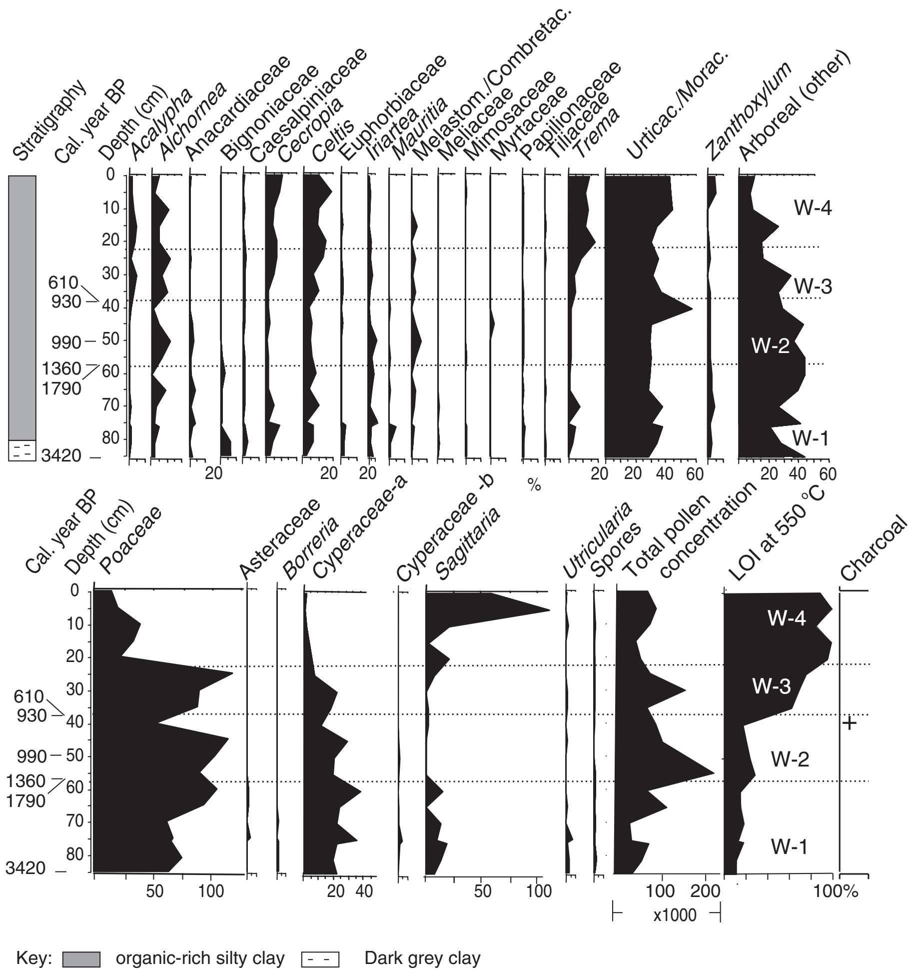

Figure 7 Percentage pollen diagram of selected taxa from Lake Werth, Peru. Also shown are sediment stratigraphy, calibrated ages, loss-on-ignition results and charcoal and pollen concentrations.

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c. 30% to > 90% organic content is gradual. Pollen concentrations have a local peak in excess of 100,000 grains cm^{-3} within this zone. *Cecropia*, *Celtis*, *Acalypha* and *Trema* all show a trend of increasing representation and Poaceae attains its highest value of the core (112%).

Zone W-4 (22–0 cm, 400–0 cal yr BP). Fibrous peat with pollen concentrations between 40,000 and 70,000 grains cm^{-3}. Poaceae pollen representation falls abruptly at the start of this zone from 100% to *c*. 20–40%. Alismataceae pollen account for > 100% near the top of the zone as *Cecropia*, *Celtis*, Urticaceae/Moraceae and *Zanthoxylum* also increase their representation.

DCA results for the complete data set

Data for all four lakes were placed in a single matrix and ordinated using DCA. The results of this analysis reveal that forest around Gentry was somewhat different from that of the other lakes (Fig. 8). The first axis of the ordination appears to segregate samples associated with basin formation at the positive extreme and regrowth forest taxa characterizing the negative extreme of the axis. All five samples with scores > 125 on Axis 1 represent the lowest samples in the cores of Parker and Gentry, or in the case of Vargas, the three lowest samples of the core. Werth has a similar, but less extreme, pattern, where the sample with the highest score on Axis 1 is the basal sample.

Axis 2 separates Gentry from the other lakes, while all the other samples sit in a dense cloud near the origin of Axis 2.

DISCUSSION

The ordinations (Fig. 3) of the fossil pollen data for each lake show some consistent trends. The samples tend to cluster according to age, so that the zones do not overlap when plotted on the first two axes. These data suggest the occurrence of pronounced environmental changes within the last 7000 years. The basal samples in Parker, Vargas and Gentry, and to a lesser extent Werth, lie at one extreme of Axis 1, suggesting that these samples are markedly different from the others. When plotted in the same matrix (Fig. 8), this pattern still holds up suggesting that these basal samples were truly different from the younger material. High proportions of Poaceae, Cyperaceae and other swamp taxa, could indicate that savannas expanded during the mid-Holocene dry period. However, diverse forest tree pollen and an absence of charcoal suggest that this was not a savanna, but a hydrologically controlled grassy swamp stage in the formation of a permanent water body, i.e. the basin was sealing.

Another commonality is that when plotted individually, samples from the last 1000 years are consistently segregated from others, suggesting that this period has been one of general change. However, when plotted together, the modern samples are clustered among other late Holocene samples, suggesting that the modern systems have analogues within the recent past of the other lakes.

Figure 8 reveals Gentry to have had the most distinct pollen history, as for much of its history it is separated from the other sites on the second axis. The presence of crop pollen and disturbance indicators at Gentry lead us to suggest that this displacement on the second DCA axis largely reflects the effects of human disturbance.

Droughts and community change

All of the lakes have discontinuous records consistent with a complex climatic history in which lakes were alternately drawn down and filled. The inter-site variation in the records of lake level reflects the influence of lake depth, catchment size, elevation relative to water-table and probable bioturbation

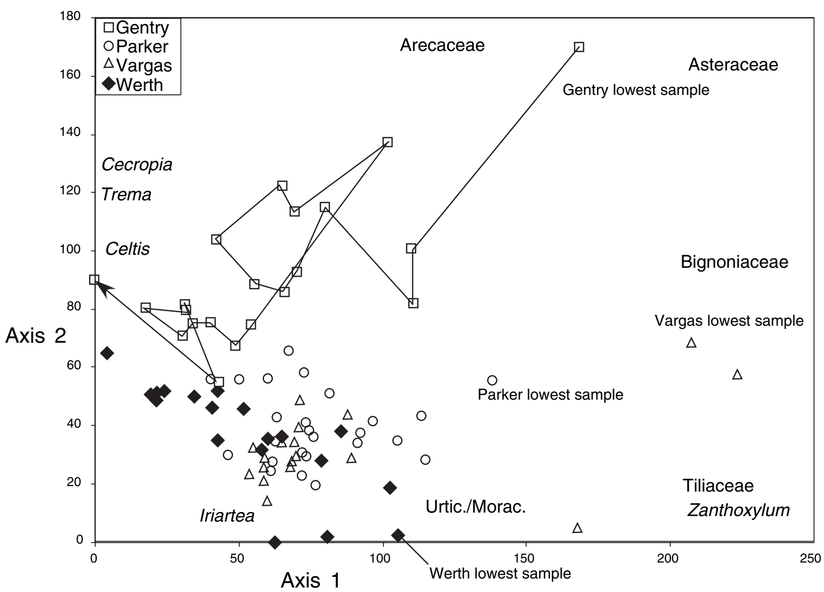

Figure 8 Results of the detrended correspondence analysis of sample data from all four lakes. Terrestrial fossil pollen data (21 commonest taxa) from lakes Gentry, Parker, Vargas and Werth were combined into a single matrix. Consecutive samples from oldest to youngest for Gentry are joined. The lowermost samples of all lakes occur to the right of the diagram but points are not joined due to strong overlap of the other samples in the lower left of the diagram. Total variance 0.8158; eigenvalues of Axis 1, 0.224 and Axis 2: 0.103. R^2 (Euclidean) Axis 1: 0.308, Axis 2: 0.343.

during lowstands. In these tropical systems in which there is very little allochthonous input, sedimentary hiatuses are often only apparent from apparent gaps in dating. During such episodes the system enters a closed carbon cycle and the algal and vegetal detritus simply oxidizes. In our experience it is not unusual to find such gaps with no physical sedimentary marker other than oxidized and broken pollen grains.

An approximate chronology of wet and dry events can be inferred from these records. Relatively wet conditions led to the formation of Vargas and Parker between 8000 and 7400 cal yr BP. A drier interval followed in which Vargas dried out. Parker appears to have dried out at about the same time, *c.* 6200 cal yr BP, that Gentry filled.

The peak of the dry event in this region appears to have been between *c.* 6200 and 4200 cal yr BP. The one datum that does not fit well with that observation is the formation of Gentry at *c.* 6200 yr BP. However, it will be noted that the sediments between depths of 87 and 97 cm in Gentry do not all contain well-preserved pollen. The sample at 95 cm contained only oxidized pollen and some charcoal. These data suggest that the surface sediments of the lake were exposed to oxidation, but the presence of charcoal suggests that the site had not been abandoned by humans (see below). When pollen is found again at 92 cm depth, the pollen spectrum looks very similar to the sample at 97 cm.

The other sample in this section of core that lacked pollen, at 90 cm depth, also lacked charcoal. When pollen is recorded again at 87 cm a substantial change is evident in both forest and aquatic taxa compared with the previous pollen-bearing stratum. Indeed, the pollen is so different that a zone boundary separates the samples at 87 and 92 cm depth. Starting at 90 cm is the longest absence of charcoal within the Gentry record, lasting until *c.* 4500 cal yr BP. It appears probable that a genuine hiatus is present in the Gentry record at 90 cm, and that the lake dried to the point where it was no longer an attractive venue for human occupation. Thus, despite initiation close to 6200 cal yr BP, the Gentry record probably also records a significant dry event centred on *c.* 5500 cal yr BP.

Taken together, the data from the four records suggest that despite evidence of this dry event, the overall pollen signature was one of mesic forest with *Cecropia*, *Celtis*, *Eschweilera* (Lecythidaceae), *Euterpe* (Arecaceae), *Geonoma* (Arecaceae), *Schefflera*, *Trema* and *Trattinickia*, as regular components of the record. Charcoal, which would be preserved even when pollen is not, disappears from the record during the driest period, strongly indicative of a lack of fire despite lowered lake levels. Thus, the lowering of lake levels that is thought to have induced Holocene savanna expansion 900 km to the east in Noel Kempff Mercado Park (NKMP), did not induce a similar response near Puerto Maldonado.

The mid-Holocene drought

The mid-Holocene drought that is documented at the Maldonado sites is coincident with a period of weakened ENSO activity (Sandweiss *et al.*, 2001; Moy *et al.*, 2002; Riedinger *et al.*, 2002) and a thermal optimum (Paduano *et al.*, 2003). If the differential insolation between the peak of the wet season and the peak of the dry season correlates with seasonality, then the southern tropics have been becoming less seasonal during the course of the Holocene (Bush & Silman, 2004). Given this confluence of climatic factors, it is probable that mid-Holocene climates may have had no exact modern analogue in many locations (*sensu* Jackson & Overpeck, 2000). Indeed, it can be argued that in terms of stress on plants, the warm dry times of the mid-Holocene may have been substantially harder to endure than the cool, moist conditions of the last glacial maximum in southern Peru (Bush *et al.* 2004).

The nearest lowland palaeoecological data previously published are for the lakes of NKMP in Bolivia (Mayle *et al.*, 2000; Burbridge *et al.*, 2004). Major commonalities and differences are observed with those records. Both locations document a lowering of lake level centred on the mid-Holocene and that the wettest time of all is within the last 800 years, but the savanna expansion evident at NKMP is not observed at Maldonado.

Human impacts and the scale of occupation

Whether Amazonian systems burn naturally or only when fires are set by humans has been the subject of debate (Sanford *et al.*, 1985; Bush *et al.*, 2000). Contemporary observations of natural forest systems within the habitat type that we document in this study are available from Cocha Cashu, Madre de Dios, Peru. In an area of *c.* 50,000 km^2, no fires have been witnessed in 40 years of observation, and a 200-year sedimentary record from Cocha Cashu contains no charcoal (M.B.B. n.d. (new datum)), save for the last 40 years when we see charcoal from wood fires from the biological station on the shore. Even Lake Werth, which receives only 1700 mm of seasonal rainfall, shows no significant charcoal input over the last 3000 years. We have a number of other unpublished cores that span 200–3000 years from south-east Peru and none contain charcoal. We infer from these observations that these forests do not burn naturally under present conditions.

Consequently, the consistent occurrence of elevated concentrations of charcoal is a strong indicator of human presence. The precise amount of charcoal will be a function of lake size, and the frequency, size, intensity and proximity of the fire (Clark & Patterson, 1997; Whitlock, 2001) and is probably less important than its consistent presence. Our suite of four lakes allows us to contrast their histories and draw inferences regarding the scale of human land use. Lake Gentry is the only lake that yielded pollen of known cultivars. The occurrence of *Zea* pollen at *c.* 3630 cal yr BP is consistent with the known spread of agriculture across Amazonia (Bush *et al.*, 1989), and two grains of *Manihot esculenta* pollen at *c.* 2400 cal yr BP strongly suggests cultivation of manioc. Both *Zea* and *Manihot* are widely cultivated by indigenous people throughout south-east Peru today.

From *c.* 4200 cal yr BP onward, Parker, Werth (*c.* 3300 cal yr BP) and Vargas (*c.* 2540 cal yr BP) fill, suggesting progressively wetter conditions. The initial adoption of *Zea mays* at *c.* 3630 cal yr BP was not noticeably correlated with a change in charcoal or *Cecropia* (a weed tree) concentrations, indeed the highest charcoal concentrations preceded maize agriculture by several thousand years.

After *c.* 800 cal yr BP lake levels appear to have been stable with much more organic sediment being deposited in all the basins than during any prior episode. Notably, despite the relatively high precipitation inferred for the near-modern period, each of the lakes shows a peak of charcoal, albeit very small at Werth, around this time.

In many Neotropical palaeoecological records where fire is not considered to be a frequent factor influencing landscapes, charcoal commonly pre-dates the adoption of *Zea*, e.g. at La Yeguada, Panama (Bush *et al.*, 1992), Ayauchi, Ecuador (Piperno, 1990), Geral, Brazil (Bush *et al.*, 2000) and Sauce, Peru (M.B.B. n.d.). This observation is wholly consistent with the view that *Zea* was added to an arsenal of existing crops, as opposed to being the signature plant around which lowland Neotropical farming developed (Piperno & Stothert, 2003).

Unlike Gentry, the other Maldonado sites yielded no crop pollen, and no middens were found close to their shores. This basic difference in land use probably drives the second axis of the DCA (Fig. 8) as it may reflect site openness. At Lake Parker, about 10 km from Gentry, the charcoal record clearly indicates human disturbance of this system, but the peaks of charcoal are uncorrelated with those in Gentry. Despite extended counts of sediment filtered to retain only the fraction > 50 μm, no *Zea* or *Manihot* pollen was found. However, cultigens that are not readily discernible from wild-type plants through palynology, e.g. beans (*Phaseolus* spp.), Brazil nut (*Bertholletia excelsa*) and *Mauritia*, could have been raised at this site, as the pollen of these genera was found in these sediments. A possible reason to burn an area but not to cultivate it would be to encourage young growth to attract game animals or to clear undergrowth from around Brazil nut trees, thereby making the nuts easier and safer to gather. Negative evidence cannot eliminate the possibility of cultivation at Parker, but it appears probable that if present it was either different from, or not as intensive as, around Gentry. Thus, we infer that both Gentry and Parker were occupied, with Gentry probably being the more intensively used system.

If we take charcoal to be a reliable indicator of occupation, it is evident that humans occupied lakes (but not swamps) very quickly. Almost as soon as Parker and Gentry stabilized as open-water systems, both initially and after marked lowstands, charcoal indicates the presence of human occupants. Lake Vargas, which formed earlier than either Parker or Gentry, was only occupied in the last millennium (Fig. 9), perhaps reflecting a more hidden location or a less desirable settlement site. Werth, which lies about 50 km from Gentry, has no apparent history of occupation. Clearly, for much of the Holocene there was a human population waiting to capitalize on favourable settlement sites in this section of Amazonia, but their search radius was probably rather local.

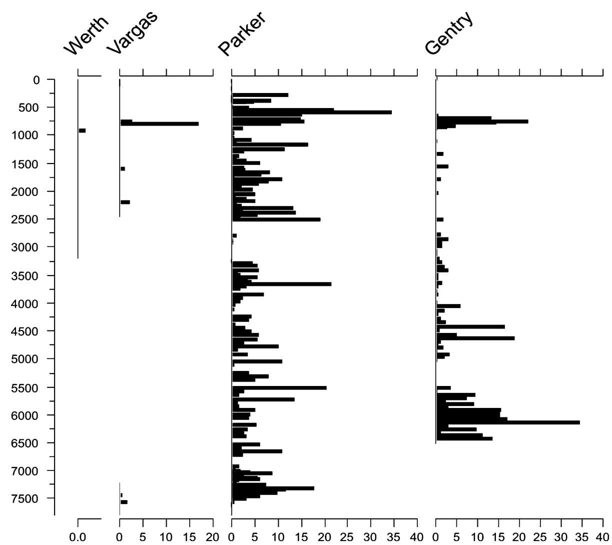

Figure 9 Sedimentary charcoal records, collected at 1-cm increments for the four lakes expressed as $mm^2\ cm^{-3}$ and plotted against time (cal yr BP).

The divergent histories of these sites suggest that the centre of occupation lay close to Gentry, that its influence encompassed Parker (*c.* 8 km from Gentry), but did not extend to Vargas, a distance of *c.* 14 km. If this is true, our results suggest that land use, particularly the use of fire, was highly localized within the landscape. Such a small scale of disturbance would be consistent with the modern 3 km radius impacted by modern indigenous peoples that practice slash and burn agriculture in western Amazonia (Apaza *et al.*, 2002) and the 9 km hunting range described by Glanz (1991).

At *c.* 600 cal yr BP an increase in fire frequency results in charcoal peaks in Vargas, Gentry and Parker. This phase may represent increased landscape manipulation and, within the error of our dating, is coincident with the rise of the Inca. Thus, the trajectory of land use may well have accelerated in the century prior to conquest in this section of Amazonia, but the continuing forest cover at all the sites would not warrant terming this a 'parkland' (Heckenberger *et al.*, 2003).

This uppermost sample at Gentry is strongly indicative of disturbance with high levels of *Cecropia*, *Trema* and *Celtis* pollen, and yet, unlike the agricultural phases, lacks charcoal. Consequently, this sample may reflect the modern regional deforestation, the construction of the nearby highway, and some timber harvesting, rather than slash-and-burn agriculture within the lake catchment.

CONCLUSIONS

Our data reinforce the importance of climatic variability within the Holocene of Amazonia, both in terms of regional ecology and also human occupation and exploitation of the landscape. Wet and dry phases are evident throughout the Holocene records of these four sites.

The dry event that dominated the mid-Holocene in the Maldonado lake records was of sufficient intensity to cause savanna expansion in ecotonal areas at the margins of Amazonia (Mayle *et al.*, 2000). However, this event did not lead to the replacement of forest by savanna in the forests near Puerto Maldonado within the last 7000 years, even though this site lies within 200 km of the modern savanna boundary.

Human occupation of the Puerto Maldonado region is certainly evident in the cultivation of domesticated crops as early as *c.* 3630 cal yr BP, and if charcoal is accepted as an indicator of human activity, then it appears that these sites have been occupied since *c.* 7200 cal yr BP. The trajectory of forest use accelerated in the last millennium, but appears to pre-date the rise of the Inca. Site abandonment probably co-occurs with depopulation following conquest (Denevan, 1976) though these sediments do not provide reliable dates for the last few hundred years.

The scale of human occupation appears to have been limited. Although Lake Gentry has a long history of agriculture, the land around nearby lakes lying just 10–15 km distant was not similarly exploited. The fossil pollen and charcoal data from these four sites also highlighted the value of investigating multiple lakes that lie close to one another, as no single record would have provided a representative picture of either the climatic or cultural events that influenced this region over the last 8000 years.

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BIOSKETCHES

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The inspiration for this special issue on Amazonian biogeography was a meeting of the Association of Tropical Biology held in Uberlândia, Brazil, 24–28 July 2005. The papers comprise several commissioned as an outcome of this meeting, alongside other unsolicited submissions to the journal