

# Holocene fire and occupation in Amazonia: records from two lake districts

Mark B. Bush<sup>1,\*</sup>, Miles R. Silman<sup>2</sup>, Mauro B. de Toledo<sup>1,4</sup>,  
Claudia Listopad<sup>1</sup>, William D. Gosling<sup>1,†</sup>, Christopher Williams<sup>1</sup>,  
Paulo E. de Oliveira<sup>3</sup> and Carolyn Krisel<sup>2</sup>

<sup>1</sup>*Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901, USA*

<sup>2</sup>*Department of Biology, Wake Forest University, Winston Salem, NC 27106, USA*

<sup>3</sup>*Department of Biological Sciences, Universidade do Guarulhos, Sao Paulo 07023-070, Brazil*

<sup>4</sup>*Marine Geology and Geophysics Department, Universidade Federal Fluminense, Niterói RJ 24.210-340, Brazil*

While large-scale pre-Columbian human occupation and ecological disturbance have been demonstrated close to major Amazonian waterways, less is known of sites in terra firme settings. Palaeoecological analyses of two lake districts in central and western Amazonia reveal long histories of occupation and land use. At both locations, human activity was centred on one of the lakes, while the others were either lightly used or unused. These analyses indicate that the scale of human impacts in these terra firme settings is localized and probably strongly influenced by the presence of a permanent open-water body. Evidence is found of forest clearance and cultivation of maize and manioc. These data are directly relevant to the resilience of Amazonian conservation, as they do not support the contention that all of Amazonia is a 'built landscape' and therefore a product of past human land use.

**Keywords:** agriculture; charcoal; fossil pollen; Peru; Brazil; pre-Columbian

## 1. INTRODUCTION

The role of pre-Columbian human activity in shaping Amazonian ecosystems has received considerable attention in the light of occupational records from the Xingu River basin, Marajos Island, and near the modern cities of Santarém and Manaus (Roosevelt 1991; Roosevelt *et al.* 1991; Heckenberger *et al.* 1999). Advocates of widespread human influence in Amazonia point to what appear to be urban centres (Roosevelt 1991; Roosevelt *et al.* 1991; Heckenberger *et al.* 1999, 2003), large earthworks in Bolivian savannahs bordering Amazonia (Mann 2000; Erickson 2001), and the widespread occurrence of soils enriched with carbon (terra preta) within Amazonia (Glaser *et al.* 2001; Lima *et al.* 2002). If Amazonia was a managed landscape prior to European contact, the biodiversity of the region has withstood substantial fragmentation, hunting and human interaction, and such manifest resilience would influence conservation decision making. While Erickson (2001) has described the Bolivian savannah landscape as having been manufactured by humans, other authors are generally more circumspect when dealing with the densely forested regions.

Major uncertainties exist in the size of the pre-Columbian human population of Amazonia, with estimates ranging from 1 to 11 million inhabitants. Similarly, the large areal extents of some archaeological

settlements, e.g. 5 km<sup>2</sup> of terra preta underlying the modern city of Santarém, have been variously interpreted as representing continuous occupation by a large population (Roosevelt 1987) or repeated resettlement and abandonment by smaller groups (Meggers 1995). Heckenberger *et al.* (2003) have argued for dense settlement and societies with strong social hierarchies with the capability to transform landscapes. The alternate view is that human endeavours in Amazonia were constrained by poor soils and that occupation was sparse, lacking the societal complexity or monuments of Andean or Central American systems (Meggers 1954, 2003*a,b*). Denevan (1996) suggested that occupation was centred on sandy bluffs overlooking navigable channels and floodplains. This interpretation of existing data suggests local alteration of landscapes extending 5–10 km around settlements, but with vast interfluvial areas where humans had little impact on the biota (Denevan 1996).

From an ecological standpoint, humans are likely to deplete animal populations and transform landscapes through burning. While it is very difficult to document the past population size of people, let alone animals, evidence of burning is well preserved in palaeoecological records. Indeed, we suggest that fire is the characterizing disturbance of human activity in much of western Amazonia and we will take its presence to be an indicator of human activity.

### (a) *Fire in Amazonian landscapes*

Human settlers modified the landscape through fire. Some parts of Amazonia are more susceptible to fire

\* Author for correspondence (mbush@fit.edu).

† Present address: Department of Earth Sciences, CEPSAR, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK.

One contribution of 14 to a Theme Issue 'Biodiversity hotspots through time: using the past to manage the future'.

than others (Nepstad *et al.* 2004) and considerable uncertainty exists over the 'natural' occurrence of Amazonian forest fires. Some researchers have found evidence of natural fire (e.g. Sanford *et al.* 1985; Saldarriaga & West 1986; Piperno & Becker 1996), whereas other data point to fire as very rare in the absence of humans (e.g. Hammond & ter Steege 1998; Turcq *et al.* 1998; Behling & Da Costa 2000; Behling 2001; Behling *et al.* 2001). In a 50 000-year palaeoecological record from the Hill of Six Lakes in northwestern Amazonia, only one sedimentary layer at 5600 calendar years before the present (yr BP) was found to contain significant amounts of charcoal, suggesting the rarity of fire in that landscape (Bush *et al.* 2004).

Piperno & Becker (1986) recorded charcoal in soils around Manaus with a concentration of ages between *ca* 900 and 1260 yr BP, and attributed these fires to natural climatic change rather than agriculture. From a nearby site, Santos *et al.* (2000) also recovered charcoal from soils with peaks between 1000 and 1300 yr BP. The period *ca* 1100–1300 yr BP was a phase of intensified El Niño activity (Moy *et al.* 2002), making it plausible that extreme drought caused fire at this time. However, some caution is needed in interpreting these data. Rather than slash and burn agriculture, less radical land management involving fire may have prevailed, e.g. that practised for Brazil nut harvesting in Peru (Phillips 1993) and *Caryocar edule* fruits by indigenous peoples in the Xingu (P. E. de Oliveira 2005, personal observation).

Nepstad *et al.* (2004) document that the forests of central Amazonia are only susceptible to natural fire during the late stages of the dry season. Under modern conditions in strongly seasonal forests, there is about a 10-day window each year when natural fire is possible. Near Manaus, the probability of fire decreases exponentially with distance from sites of human occupation (Laurance & Williamson 2001). In Peruvian Amazonia, indigenous people find it difficult to burn the forest at any time.

Evidence of the rarity of fire in western Amazonia comes from historical and palaeoecological observations. Cocha Cashu in Manu National Park lies less than 200 km from the western Lake District and has been continuously monitored for the past 40 years. In that time, no fire has been documented within the approximately 50 000 km<sup>2</sup> reserve. The only charcoal recovered from the Cocha Cashu lake sediments were fragments derived from wood burned since 1968 by the lake-shore field station (M. R. Silman, unpublished core data). Sediment cores raised from three oxbow lakes along the Madre de Dios, all of which span the past 220–700 years contain no charcoal (Listopad 2001). Similarly, the *ca* 3300-year record from Lake Werth (below) contains no evidence of local forest fires. We conclude from these observations that under modern conditions, fire is not a natural phenomenon within this forest area.

Three factors combine to provide the probability that a given site is susceptible to fire: the amount of precipitation; the strength of the dry season; and the amount of human activity. Once an area has burned, however, successive burning is promoted by increased dead biomass, reduced canopy cover and a drier litter layer (Nepstad *et al.* 2004). Such fires are documented

in lake records in the absolute concentration of charcoal in lake sediment. However, as lake size and taphonomic processes influence rates of charcoal deposition (Whitlock *et al.* 1997; Whitlock & Larsen 2001), comparisons of concentration to infer intensity of land use are most robust within a lake record, rather than between lake records.

Although landscape alteration is clearly going to have occurred around known archaeological sites, the extent to which those sites are representative of other portions of Amazonia is unknown. Consequently, the spatial and temporal scale of landscape alteration in previously undocumented settings may provide an alternative image of Amazonian occupation. We present data from two Amazonian lake districts that document human occupation, and use the charcoal and pollen records from those sites to gauge the spatial and temporal extent of landscape alteration at those locations. In particular, we ask 'did human occupation result in widespread landscape modification at these two widely separated Amazonian sites?' or, as hypothesized by Denevan (1996), is human disturbance centred on particular features of the landscape?

## 2. MATERIAL AND METHODS

### (a) Study areas

A paucity of long Holocene palaeoecological records exists in Amazonia, but here we report on two suites of cores raised to investigate climate change in ecologically sensitive areas of Amazonia (Listopad 2001; M. B. de Toledo 2004, unpublished Ph.D. thesis). Sites were selected to provide lakes that were not directly influenced by rivers, lay within terra firme forest and where replication could be achieved within a small geographical area. A western lake district (hereafter western lakes) near Puerto Maldonado, Peru, that comprised lakes Gentry, Vargas, Parker and Werth, and an eastern lake district (hereafter eastern lakes) near Prainha, Brazil, that comprised lakes Geral, Santa Maria and Saracuri, were selected for study.

The western lakes lie within a lake district containing approximately 50 lakes and swampy depressions (approx. 12.5° S, 69.0° W; figure 1a). The lake district lies at approximately 230 m elevation and all of the lakes are relatively small, approximately from 0.3 to 2 km in diameter and are approximately 1–3 m deep. The origin of the lakes is unknown, but they lie at the highest points on the rolling landscape, outside fluvial influence, and are underlain by sands and clays.

The lakes lack inflowing streams and their permanence is indicated by the presence of fishes. The lakes appear to be mesotrophic and are fringed by beds of *Sagittaria*, *Pontederia* and *Eichornia*. The forests in the region are upper-Amazonian rainforest and have been extensively documented, e.g. Pitman *et al.* (2001) and are rich in *Calycophyllum*, *Calophyllum*, *Cecropia*, *Cedrela*, *Ceiba*, *Dipteryx*, *Ficus* (35 species) and *Poulsenia* (Foster 1990). The palms *Iriartea deltoidea* and *Astrocaryum murumuru* are the commonest stems in the forest (Pitman *et al.* 2001). Of note is the local abundance of Lecythidaceae (particularly *Bertholletia excelsa* and *Couratari* spp.) in the forests. Temperatures are relatively constant with a mean of 25°C, but the lake district lies across a region of sharply changing precipitation ranging from approximately 2000 mm yr<sup>-1</sup> in the south to approximately 1700 mm yr<sup>-1</sup> in the north. Similarly, there is some variability in the dry season which ranges from two to four months in duration. A modern road passes closest to Lake Gentry, and on a knoll

beside a stream within 1 km of Gentry is a modern farmhouse. The occupant of the farm pointed out that the knoll was rich in stone tools and pottery, and he showed us his collection of axe heads and other stone tools that he had found close to his house. No formal description was attempted for this site; we report it to emphasize some prior use and occupation of the site. No archaeological evidence of occupation was noted for the other lakes.

The eastern lakes lie between 20 and 30 m in elevation on a north-south transect perpendicular to the Amazon River (figure 1*b*). The three lakes occupy old river valleys and probably filled as sea-level rose in the early Holocene. These elongate lakes range in size from approximately 400 × 100–3000 × 1000 m. *Mauritia* and *Mauritiella* were common on shorelines and in swamps. Mean annual temperature is 27°C and rainfall is approximately 2200 mm per annum over an eight and nine month wet season (Instituto Brasileiro de Geografia e Estatística 1990). Though this climate could support tropical semideciduous forest, the local vegetation is a savannah-forest mosaic. The origin of the savannah is unknown and could be the result of edaphic factors or a long history of human landscape alteration (Prance & Schubart 1977).

Saracuri is completely enclosed by forest, with just some recent deforestation on the northern shoreline. Parts of the Santa Maria catchment are recently deforested, but a patch of tall dry forest lies within its catchment. Geral is an elongated lake running approximately east-west. Along its northern shore is forest, with savannah along its southern shore. Today, Geral is extensively used for leisure and fishing, receiving visitors from Prainha (28 km away). The other lakes are used by cattle and for fishing by the owners, but show no other evidence of human use. The fossil pollen and phytolith history of Geral have previously been described (Piperno & Pearsall 1998; Bush *et al.* 2000).

#### (b) Field and laboratory techniques

Between 1990 and 2001, cores were raised from the centre of each lake using a Colinvaux-Vohnout coring rig from a raft of rubber boats. The core from Geral was initially analysed at the Smithsonian Tropical Research Institute, Panama, and later, like the others, at the Florida Institute of Technology. Pollen analysis followed standard protocols (Stockmarr 1971; Faegri & Iversen 1989), and is reported in Bush *et al.* (2000; *in press*) and M. B. de Toledo (2004, unpublished Ph.D. thesis). All Poaceae pollen grains identified as maize had a distinctive surface pattern and a diameter greater than 90 µm (note that this is a more exacting definition than often used). The pollen sum is based on a minimum of 300 terrestrial pollen, with the exception of Geral, which is based on 200 terrestrial pollen. Aquatic taxa (e.g. Cyperaceae, *Ludwigia*, Alismataceae and Pontederiaceae) were excluded from the pollen sum, but are expressed as a percentage of the terrestrial pollen.

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 National Institutes of Health-image (Clark & Hussey 1996; Clark & Patterson 1997). Diagrams were plotted using C2 (Steve Juggins, University of Newcastle).

### 3. RESULTS AND DISCUSSION

#### (a) Chronology

With the exception of Geral, the chronologies of all the lake records are supported by at least five <sup>14</sup>C accelerator mass spectrometry (AMS) dates (see table 1). The Geral chronology is based on two bulk

carbon dates. All dates were calibrated using Calib 5.1 (Stuiver & Reimer 1993) using the Southern Hemisphere correction and are reported as yr BP.

#### (b) Western lakes

Climatic fluctuations of the Holocene are evident in these records. Although three of the lakes (Vargas, Parker and Gentry) formed between 8000 and 6000 yr BP, this was not a uniformly wet period. Consistent with other regional data (Bush *et al. in press*), a mid-Holocene dry event influenced the region, but was interrupted by wet episodes, presumably when the lakes filled (Paduano *et al.* 2003). The lakes show different levels of sensitivity to drought, with Vargas most sensitive, then Parker, and Gentry the least sensitive. However, even Gentry was susceptible to drying and prior to ca 4800 yr BP exhibited at least two brief phases when pollen was oxidized from the sediments. Another period of apparently slow sedimentation between ca 1270 and 2800 yr BP may point to intermittent accumulation, although high pollen concentrations suggest that this may simply have been a time of little sediment input; otherwise the Gentry record appears to have a continuous history of pollen accrual. The last lake to form was Werth, which started to accumulate sediment ca 3400 yr BP, and deepened at ca 900 yr BP.

Once the lakes had formed fully, they provide pollen records with greater than 70% arboreal pollen throughout their history (figure 2). Only Gentry showed evidence of agriculture, with *Zea* pollen found between 3700 and 500 yr BP and two grains of *Manihot* pollen at ca 2400 yr BP. Charcoal was most abundant in Gentry, ranging between 1 and 34 mm<sup>2</sup> cm<sup>-3</sup> throughout much of the record. Notably, charcoal was absent during the second of the oxidizing phases at ca 5000 yr BP.

Lake Parker also contained charcoal through much of its history, including the time immediately prior to the formation of Gentry. Charcoal concentrations in Parker were generally about half those of Gentry, between approximately 0.5 and 17 mm<sup>2</sup> cm<sup>-3</sup> (figure 2). Lake Vargas contains no charcoal for most of its history, except a strong spike of charcoal with approximately 17 mm<sup>2</sup> cm<sup>-3</sup> at ca 1000 yr BP. The Lake Werth record contains no charcoal except for three tiny fragments at ca 800 yr BP.

#### (c) Eastern lakes

The eastern lakes, Saracuri, Santa Maria and Geral all formed between 8200 and 8400 yr BP. The previously reported history for Geral (2000; Piperno & Pearsall 1998) is substantiated and supplemented by the new analyses.

The small basin of Santa Maria provides a sensitive proxy for lake level change. High modern aquatic pollen abundances are due to a 40 m wide floating mat of marshland species. Poaceae pollen rises and falls synchronously with the aquatics, indicating that at this site Poaceae pollen are probably derived from the marsh fringe. Notably, Poaceae percentages range as high as 85% at Santa Maria, whereas they seldom rise above 12% at the other two lakes. Saracuri provides a remarkably stable pollen record throughout its history (figure 3) and



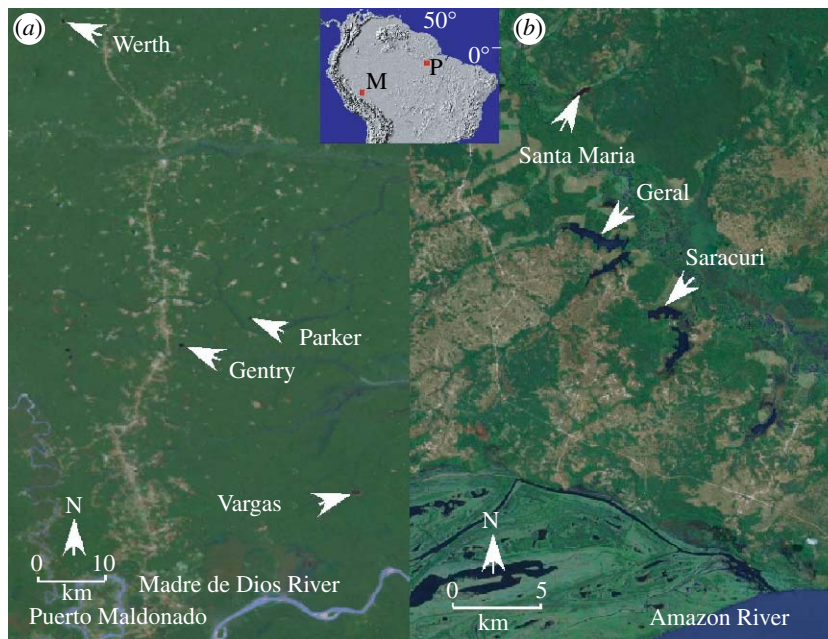


Figure 1. Satellite images showing the location of the (a) Maldonado lakes, southeastern Peru and (b) the Prainha lakes relative to major rivers and South America. Forest is shown as darker areas, with brown areas being savannah or cerrado. Charcoal is expressed as  $\text{mm}^2$  per  $\text{cm}^3$ . Latitude and longitude of Gentry  $12^\circ 10' 38.31''$  S;  $69^\circ 05' 51.54''$  W and Geral  $1^\circ 38' 48.85''$  S;  $53^\circ 35' 43.9''$  W.

contrasts with the post-4000 yr BP portion of the Geral record, lacking high proportions of Poaceae, high charcoal content and the pollen from known cultivars. The divergence of the Poaceae curve from Geral with that of Saracuri is consistent with the onset of agriculture and probably reflects human activity around Geral.

Geral is the only lake of this trio in which *Zea mays* pollen was found. Pollen and phytoliths of *Zea* are found consistently after *ca* 4030 yr BP and prior to *ca* 850 yr BP. A phase of more active forest burning is evident in both the local charcoal reported here (figure 3) and a doubling of the concentration of charred *Heliconia* phytoliths at this level (Piperno & Pearsall 1998). Clearly, while cultivation of maize may have taken place on the shoreline and in seasonally exposed shallows (Roosevelt 1980; Matheny & Gurr 1983), there was also clearance of adjacent forest. Santa Maria and Saracuri both contained charcoal, including samples predating the first evidence of charcoal at Geral but at lower concentrations than in Geral. Within the period of known crop cultivation, charcoal concentrations at both Santa Maria and Saracuri fall from their mid-Holocene highs, whereas those of Geral show a much lesser decline. Indeed, the early Holocene peaks of concentration are slightly higher at Santa Maria (as befits a small basin) than at Geral, but fall to about one-fifth those of Geral post-4000 yr BP, suggesting much lower fire frequency than at Geral.

#### (d) The charcoal record

A regional drought influenced western and southern Amazonia between *ca* 6200 and 3400 yr BP (Servant *et al.* 1981; Mayle *et al.* 2000; Listopad 2001; Mayle & Beerling 2004), though its occurrence in central Amazonia is much less clearly defined (Bush *et al.* 2000; Behling *et al.* 2001; Listopad 2001; M. B. de Toledo 2004, unpublished Ph.D. thesis). During this period, fire frequency in the western lakes does not appear to be markedly different to other periods of the

Holocene even though drought causes lake level to fall, exposing the mud–water interface. While organic material fails to accumulate and pollen is oxidized, charcoal continues to accumulate as it oxidizes very slowly. In none of the lakes is there evidence of a charcoal spike associated with a time of low pollen concentrations. Fires in these forests probably accompanied human activities and dry episodes caused site abandonment. At Gentry, the few samples that contained no pollen also contained no charcoal. Similarly, the record from Vargas overlaps with that of Parker between *ca* 7500 and 7000 yr BP and shows no peak of charcoal associated with the highest proportion of Poaceae. We infer that fire was rare or absent from this setting in the absence of human disturbance.

Vargas was the first lake to form and appears to have been briefly occupied and then abandoned. The abandonment is approximately coincidental with the colonization of Lake Parker and the first charcoal evident in that record. As Gentry filled, it was quickly occupied and the fire intensity and frequency became greater than that of any of the other sites.

In the eastern lakes, all three lakes contain some charcoal, but the lake that yielded crop pollen had the most consistent occurrence of relatively high concentrations of charcoal. Although Geral shows a more consistent fire history than the other two lakes, even the forested sites of Santa Maria and Saracuri were prone to fire, especially in the early Holocene. The highest charcoal peaks in those records are between 6900 and 7500 yr BP. The Geral record is not as well dated, but a peak of charcoal 6700 and 7200 yr BP is seen to overlap with the fire peak at other sites.

At Saracuri and Santa Maria, diminishing charcoal inputs indicate that fire becomes relatively rare *ca* 6800 yr BP. Between 6200 and 4500 yr BP, an oscillation in the aquatic and Poaceae pollen signatures, and a spike of charcoal at Santa Maria, suggest

Table 1. Radiocarbon data and calibrated ages for lakes Vargas, Parker, Gentry, Werth, Geral, Saracuri and Santa Maria.

lab number	depth (cm)	$\delta^{13}\text{C}$ ‰	$^{14}\text{C}$ age (yr)	calibrated age (yr BP)	median probable age (yr)
<b>Gentry</b>					
NSRL-11997	33	-22.35	> modern	—	0
NSRL-11998	43	-25.06	940 ± 40	743–902	770
NSRL-11999	49	-23.48	2250 ± 30	2149–2306	2270
NSRL-12001	51	-24.03	2610 ± 50	2504–2749	2620
NSRL-12000	77	-24.33	4070 ± 35	4429–4522	4490
NSRL-12002	106	-24.50	5440 ± 40	6033–6279	6230
<b>Parker</b>					
OS-38415	50	-25	525 ± 25	507–528	520
CAMS 109894	110	-25	2815 ± 35	2789–2918	2830
OS-38416	130	-22.61	3530 ± 35	3693–3827	3750
CAMS 109895	167	-25	5850 ± 35	6546–6658	6600
OS-38417	178	-26.07	6140 ± 45	6809–7144	6950
OS-35829	216	-27.11	6410 ± 45	7181–7413	7290
<b>Vargas</b>					
OS-38418	55	-27.2	> modern	—	0
OS-38419	80	-29.86	945 ± 30	763–902	840
OS-39955	88	-28.74	1390 ± 30	1189–1298	1280
OS-39954	110	-28.53	6300 ± 45	7029–7254	7200
OS-35343	166	-24.43	7060 ± 60	7762–7932	7830
<b>Werth</b>					
CAMS -74839	37	-25	580 ± 70	506–628	540
CAMS -75227	37	-27	1020 ± 50	803–930	840
NSRL-11994	50	-14.94	1070 ± 35	914–964	940
CAMS -75228	57	-27	1470 ± 40	1294–1345	1320
CAMS -74982	57	-25	1850 ± 40	1633–1813	1750
NSRL-11994	90	-25	3200 ± 45	3274–3442	3370
NSRL-11995	100	-18.93	130 ± 35	0–250	140
NSRL-11996	140	-23.19	12 750 ± 65	14 934–15 175	15 100
<b>Geral</b>					
β-41654	375–387	-28.9	5760 ± 90	6403–6630	6540
β-39702	542–551	-28.2	7500 ± 100	8179–8369	8270
<b>Santa Maria</b>					
OS 24122	172	-25	2960 ± 45	2960–3141	3050
OS 24123	240	-25	3450 ± 35	3585–3690	3640
OS 24124	407	-25	4660 ± 40	5093–5448	5270
OS 24125	528	-25	6180 ± 40	6938–7156	7050
OS 24126	570	-25	6770 ± 45	7513–7620	7560
CURL-5386	806	-25	6740 ± 45	7506–7592	7550
<b>Saracuri</b>					
OS-38383	70	-25	785 ± 25	662–716	690
OS-38384	263	-25	4130 ± 30	4448–4784	4610
OS-38385	355	-25	3780 ± 30	3989–4146	4070
OS-38386	462	-25	4390 ± 35	4850–4960	4910
OS-38387	666	-25	5980 ± 45	6674–6792	6730
CURL-5385	859	-25	7690 ± 75	8378–8536	8450

the possibility of a somewhat drier or more fire-prone system, although the lake does not dry out. At Geral, increased charcoal and *Cecropia* abundance characterize this period, suggesting increased disturbance and gap formation in the local forests, probably attributable to human activity. At Saracuri, a very slight increase in charcoal abundance is coincident with a modest increase in Poaceae pollen. Taken together, these data suggest a period of increased human activity and possibly a more flammable forest under drier conditions. These data are consistent with a rather weak manifestation of the mid-Holocene dry event documented in western Amazonia and the High Andes (Bush *et al.* 2005).

The charcoal record of Geral is wholly consistent with that of the phytolith record (Piperno & Pearsall 1998). *Heliconia* is a genus generally associated with forest gaps and clearings. Most (70%) of the *Heliconia* phytoliths recovered at *ca* 6500 yr BP were charred, as were a substantial proportion of Poaceae and leaf phytoliths from arboreal species. These data strongly suggest that fire was used to clear forests near the lake. While this evidence clearly indicates human activity, the first occurrence of landscape alteration probably dates to at least 7700 yr BP, i.e. the first occurrence of charcoal in the record. One possibility is that land use intensified around 6000 years ago, coinciding with the increase in *Cecropia* pollen and the nearly

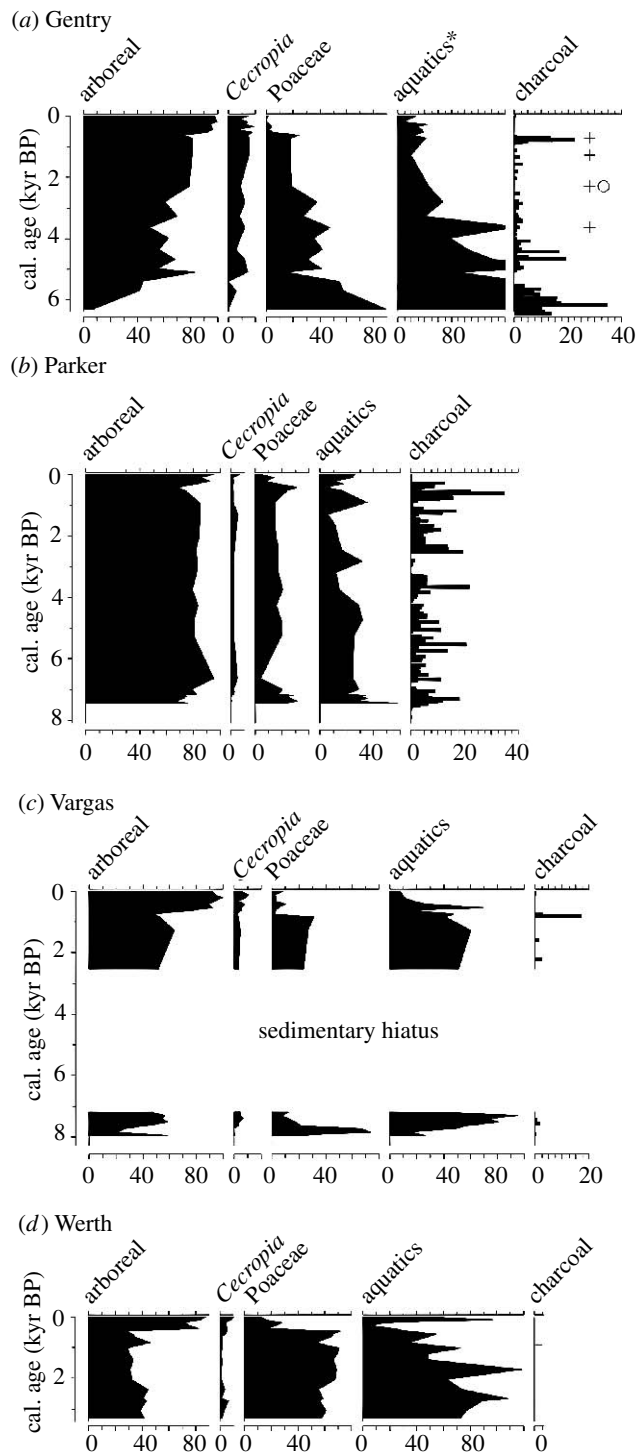


Figure 2. Fossil pollen summary percentage data and charcoal for the Maldonado lakes. Summary groups are: arboreal (sum of more than 200 types), Poaceae, aquatics, crops (plus, *Zea*; open circle, *Manihot*) and charcoal, plotted against time. Asterisk, change of scale for Gentry aquatics (double other percentage scales); dashed line, trace presence of charcoal (Werth). Charcoal is expressed as mm<sup>2</sup> per cm<sup>3</sup>.

contemporaneous occurrence of burned phytoliths and Poaceae pollen. However, it can also be argued that prior to the formation of an open body of water at the coring site, the deposition of microfossils may have reflected so local a source that land use beyond the immediate vicinity of the sample site cannot be detected. Hence, we cannot specify a time for the onset of disturbance at Geral.

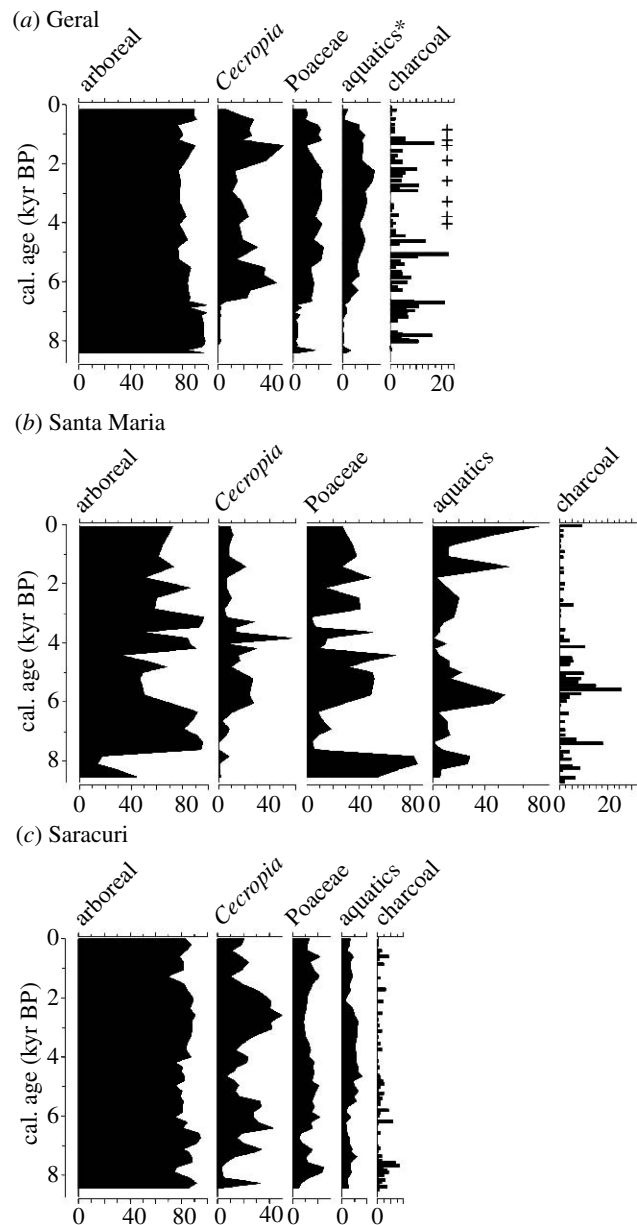


Figure 3. Fossil pollen summary percentage data and charcoal for the Prainha lakes. Summary groups are: arboreal (sum of more than 150 types), Poaceae, aquatics, crops (plus, *Zea*) and charcoal, plotted against time.

(e) *The scale of impact*

Prior to what may have been a single local fire event at Vargas, the scale of occupation appears to be consistent with modern anthropological observations that indigenous people manipulate relatively small territories. The actively managed area is much smaller than the hunting range. Studies of the Secoya–Siona in Ecuador revealed an occasional hunting range as large as 2500 km<sup>2</sup>, with 590 km<sup>2</sup> being heavily used (Vickers 1988). The Secoya–Siona hunters live in the black-water systems of the Cuyabeno River, and hunting ranges in the fertile white-water systems of Peruvian Amazonia might be smaller. The Tsimane of northern Bolivia concentrate their farming and hunting activity within 3 km of their settlement (Apaza *et al.* 2002). Carneiro (1970) has suggested that a radius of approximately 5 km could support a sedentary population of 500 through swidden agriculture indefinitely. We have no way to estimate



population size around Geral or Gentry. If we assume that these lakes were the centre of occupation, it is evident that the strength of human influence on the landscape decreased markedly with increasing distance from them.

After several thousand years of apparent use, the first palynologically identifiable crop is found in the sediments of Gentry. Only Gentry provided direct evidence of cultivation with pollen of *Zea* being found regularly between 3700 and 500 yr BP and manioc at ca 2400 yr BP. There is no clear spike in charcoal associated with the onset of maize cultivation; therefore, the field systems were already cleared or the cultivation took place on exposed mud when lake levels were low. The onset of maize cultivation coincides with a period of very slow sedimentation at Gentry, consistent with intermittent sediment accumulation and lowered lake levels, offering the opportunity to cultivate exposed wetlands. Detection of maize pollen at this time may not be a coincidence, as such large pollen grains (greater than 90 µm) are poorly dispersed, and cultivation closer to the sampling point improves the probability of recovering the fossil grain. Taking the charcoal and crop data together, we infer that humans have occupied this region of Amazonia for more than 8000 years, and through the use of fire they have altered the landscape at least at a local level. From our data, we cannot determine whether the occupation was seasonal or permanent, though the abundance of pottery shards on the ridge beside Gentry suggests a degree of permanence.

The sequential occupation of Vargas (and its abandonment), Parker and Gentry suggests that inhabitants were continually taking advantage of better home sites and may have abandoned these sites during the peak drought event at ca 5000 yr BP. If we are correct that Gentry was the centre of the occupation, we can compare the relative impacts to Parker, Vargas and Werth in terms of distance from the primary settlement.

The distance between Gentry and Parker is 9.5 km and between Gentry and Vargas is 17.5 km. Parker appears to have been used fairly extensively, but perhaps less intensively than Gentry, as no evidence was found of crop cultivation. Only in the last millennium were Gentry, Parker and Vargas simultaneously occupied. This expansion is coincident with the major Xingu landscape transformation (Heckenberger *et al.* 2003), but we note that it did not extend to the more remote setting of Lake Werth, 50 km from Gentry, which was never impacted by human occupation.

A similar image emerges from the eastern sites. If it is assumed that the long history of agriculture at Geral indicates that this lake formed the centre of local occupation, the distance to the adjacent lakes provides a scale of local impact. Saracuri at 5 km distance and Santa Maria at 6.7 km distance were both lightly used. No evidence exists to suggest that sites more than 5 km from the centre of occupation were heavily modified, though undoubtedly they would have been the site of hunting activity. Although the eastern sites lie within 150 km of the major pre-Columbian settlements around Santarém, that pattern of large landscape transformation is not seen in these records.

Our data are entirely consistent with the observation by Smith (1980) that the average size of terra firme terra preta deposits was approximately 1.4 ha, whereas

riverside sites averaged 21.2 ha. This observation supports a history of patchy disturbance, with riverside settings not being typical of settings remote from rivers. Smith (1980) specifically noted that sites near the confluence of the Rio Negro and the Solimoes rivers and on the Xingu were particularly large. Consequently, we conclude that while disturbance was probably profound at a landscape level around major settlements, such localities should not be used to generalize about the state of Amazonia as a whole.

#### 4. CONCLUSIONS

We offer the first landscape-scale view of disturbance at two sites in Amazonia and see long histories of disturbance at what appears to be a central location, with relatively small impacts on nearby systems and no apparent impacts on a system 50 km away. While these data do not support the contention of widespread landscape alteration, we note a considerable increase in human alteration of the landscape of the western lakes in the millennium prior to abandonment. Clearly, palaeoecological evidence exists for a population collapse at many sites across Amazonia and in isthmian regions of Central America (e.g. Bush *et al.* 1989; Piperno 1990; Bush & Colinvaux 1994).

In our experience of studying more than 30 lake records from Amazonia, a general rule of thumb has emerged: if the lake has modern use, has a road to it or has a settlement beside it, there is a very good probability of finding a long record (thousands of years) of disturbance. If, on the other hand, the lake is remote from modern society, it probably has a history lacking the characteristic signature of human activity. Denevan's (1996) bluff model of occupation often coincides with the sites of modern occupation and hence our observations align well with his model. Although exceptions can always be found, modern use of an area is a powerful predictor of past human activity.

We observe that the extent of deforestation around the lakes that we discuss in this paper, and also the minimally seasonal locations of Kumpak<sup>a</sup> (Liu & Colinvaux 1988) and Ayauch<sup>i</sup> (Bush *et al.* 1989) in Ecuador, was probably considerably less than around lakes in Central America with comparable histories of occupation, e.g. La Yeguada (Piperno *et al.* 1991) and Lake Wodehouse (Bush & Colinvaux 1994). It may be that the sites with very strong seasonality, which includes the Xingu, were more extensively impacted than less seasonal settings. We suggest that extrapolating from known areas of intense occupation to infer that most of Amazonia was a parkland in 1492 AD (458 yr BP) would be unwise. Rather we suggest that the highly heterogeneous history of land use, exploitation levels and population densities in Amazonia should be recognized, as these probably varied widely across this vast region in response to local soils, climate and potential protein sources. We now know that tropical forests have been subject to considerable climate change throughout the Quaternary. Forests of the Holocene are different in relative species abundance and productivity than they were during much of the Pleistocene. And even within the Holocene, natural

disturbance cycles such as droughts and disease may have played an important role in reshaping communities.

Hence, pre-Columbian Amazonian landscapes that differ from those of today could have been due to both direct and indirect human influence, natural causes, or most likely, some combination of all of these. Direct human actions include land conversions such as felling trees and setting fires. The temporal and spatial scales of these disturbances need to be resolved across the range of Amazonian landscape types. Indirect actions include hunting, introduction of exotic species that then modify a landscape or a disease that crosses from one host to another. Megafauna have large and clear landscape-level effects on forest structure and composition in systems where they still exist. What was the effect of their extinction on Amazonian forests? If, as has been suggested, the loss of megafauna was attributable to humans, then the case for a human modification of Amazonian landscapes is strengthened, although not on the time- or spatial-scale of the current archaeological debate.

Natural disturbance in the Holocene of Amazonia was probably also profound. While there is increasing documentation of millennial scale droughts (see §3*d*), contemporary studies indicate the potential importance of unexplained changes in animal abundance. In the 1980s, white-lipped peccaries disappeared, apparently stochastically, from an area of more than 70 000 km<sup>2</sup> for 12 years. The absence of this major seed predator resulted in a surge in recruitment of the dominant rainforest tree species (Silman *et al.* 2003, Wyatt & Silman 2004), an imprint that will last for decades, perhaps centuries, on this region.

Two potentially crucial differences exist between pre-Columbian human and natural disturbance in many areas of Amazonia. The first is the scale of disturbance. Modern studies of fragmentation show that duration and areal extent are critically important to post-abandonment succession (Laurance *et al.* 2002). Were the landscapes created by pre-Columbian occupants of Amazonia on the scale of a large tree-fall gap, or orders of magnitude larger? How long did disturbance persist on the same location? The second is the introduction of fire. Repeated burning transforms rainforest communities, whereas a single fire has lesser effects (Cochrane & Schulze 1998; Haugaasen *et al.* 2003). Determining whether the same patch of forest was burned repeatedly or whether there were long periods of recovery between events is an important question that needs to be resolved before making predictions of human impacts in any locale.

The conservation message that emerges from this and other palaeoecological studies is that many forests may be only one or two tree generations away from a period of land use and that in such areas populations are unlikely to be equilibrating (e.g. Foster *et al.* 2002). However, the type of mixed land use of the past was utterly different to the deforestation that accompanies modern ranching and soyabean farming. Away from the largest settlements, it is probable that gaps created by pre-Columbian farmers were closer to the scale of natural blowdowns, i.e. 1–10 ha, rather than the thousands of hectares created by agro-industry. Consequently, seed sources remained locally available and biodiversity was not reduced.

Modern biodiversity and forest composition are not a product of land management, but have persisted despite it.

We are grateful to Paul Colinvaux for his role in directing the coring of Lake Gentry and to Chengyu Weng, Emilio Ancaya and Matthew Scriptor for coring lakes Parker and Vargas. Carol Mitchell and Rolando Soto are thanked for logistical support in Peru. Hermann Behling and an anonymous reviewer provided thoughtful comments that strengthened this paper. This work was funded by NSF grants DEB 9732951, 0237573 (M.B.B.) & 0237684 (M.R.S.) and CNPq (doctoral scholarship 200065/99-8) (M.B.T.).

## REFERENCES

- Apaza, L., Wilkie, D., Byron, E., Huanca, T., Leonard, W. & Pérez, E. 2002 Meat prices influence the consumption of wildlife by the Tsimane Amerindians of Bolivia. *Oryx* **36**, 382–388. (doi:10.1017/S003060530200073X)
- Behling, H. 2001 Late Quaternary environmental changes in the Lagoa da Curuça region (eastern Amazonia, Brazil) and evidence of *Podocarpus* in the Amazon lowland. *Veg. Hist. Archaeobot.* **10**, 175–183. (doi:10.1007/PL00006929)
- Behling, H. & Da Costa, M. L. 2000 Holocene environmental changes from the Rio Curuá record in the Caxiuaná region, eastern Amazon Basin. *Quat. Res.* **53**, 369–377. (doi:10.1006/qres.1999.2117)
- Behling, H., Keim, G., Irion, G., Junk, W. & Nunes de Mello, J. 2001 Holocene environmental changes in the central Amazon Basin inferred from Lago Calado (Brazil). *Palaeogeogr. Palaeoclim. Palaeoecol.* **173**, 87–101. (doi:10.1016/S0031-0182(01)00321-2)
- Bush, M. B. & Colinvaux, P. A. 1994 A paleoecological perspective of tropical forest disturbance: records from Darien, Panama. *Ecology* **75**, 1761–1768. (doi:10.2307/1939635)
- Bush, M. B., Piperno, D. R. & Colinvaux, P. A. 1989 A 6000 year history of Amazonian maize cultivation. *Nature* **340**, 303–305. (doi:10.1038/340303a0)
- Bush, M. B., Miller, M. C., De Oliveira, P. E. & Colinvaux, P. A. 2000 Two histories of environmental change and human disturbance in eastern lowland Amazonia. *The Holocene* **10**, 543–554. (doi:10.1191/095968300672647521)
- Bush, M. B., De Oliveira, P. E., Miller, M. C., Moreno, E. & Colinvaux, P. A. 2004 Amazonian paleoecological histories: one hill, 3 watersheds. *Palaeogeogr. Palaeoclim. Palaeoecol.* **214**, 359–393.
- Bush, M. B., Hansen, B. C. S., Rodbell, D., Seltzer, G. O., Young, K. R., Léon, B., Silman, M. R., Abbott, M. B. & Gosling, W. D. 2005 A 17,000 year history of Andean climatic and vegetation change from Laguna de Chocho, Peru. *J. Quat. Sci.* **20**, 703–714. (doi:10.1002/jqs.983)
- Bush, M. B., Listopad, M. C. S. & Silman, M. R. In press. Climate change and human occupation in Peruvian Amazonia. *J. Biogeogr.*
- Carneiro, R. 1970 Hunting and hunting magic among the Amahuaca of the Peruvian Montaña. *Ethnology* **9**, 331–341.
- Clark, J. S. & Hussey, T. C. 1996 Estimating the mass flux of charcoal from sedimentary records: effects of particle size, morphology, and orientation. *The Holocene* **6**, 129–144.
- Clark, J. S. & Patterson, W. A. I. 1997 Background and local charcoal in sediments: scales of fire evidence in the paleorecord. In *Sediment records of biomass burning and global change*, vol. 51 (eds J. S. Clark, H. Cachier, J. G. Goldammer & B. Stocks). *NATO ASI series 1: global environmental change*, pp. 23–48. Berlin, Germany: Springer.
- Cochrane, M. A. & Schulze, M. D. 1998 Forest fires in the Brazilian Amazon. *Conserv. Biol.* **12**, 948–950.



- Denevan, W. M. 1996 A bluff model of riverine settlement in prehistoric Amazonia. *Ann. Assoc. Am. Geogr.* **86**, 654–681. (doi:10.1111/j.1467-8306.1996.tb01771.x)
- Erickson, C. L. 2001 Pre-Columbian roads of the Amazon. *Expedition* **43**, 21–30.
- Faegri, K. & Iversen, J. 1989 *Textbook of pollen analysis*. Chichester, UK: Wiley.
- Foster, R. B. 1990 The floristic composition of the Rio Manu floodplain forest. In *Four neotropical rainforests*, vol. 627 (ed. A. H. Gentry), pp. 99–111. New Haven, CT: Yale University Press.
- Foster, D. R., Clayden, S., Orwig, D. A., Hall, B. & Barry, S. 2002 Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA. *J. Biogeogr.* **29**, 1359–1379. (doi:10.1046/j.1365-2699.2002.00760.x)
- Glaser, B., Haumaier, L., Guggenberger, G. & Zech, W. 2001 The 'Terra Preta' phenomenon: a model for sustainable agriculture in the humid tropics. *Naturwissenschaften* **88**, 37–41. (doi:10.1007/s001140000193)
- Hammond, D. S. & ter Steege, H. 1998 Propensity of fire in Guianan rainforests. *Conserv. Biol.* **12**, 944–947.
- Haugaasen, T., Barlow, J. & Peres, C. A. 2003 Surface wildfires in central Amazonia: short-term impact on forest structure and carbon loss. *For. Ecol. Manag.* **179**, 321–331. (doi:10.1016/S0378-1127(02)00548-0)
- Heckenberger, M. J., Kuikuro, A., Kuikuro, U. T., Russell, J. C., Schmidt, M., Fausto, C. & Franchetto, B. 2003 Amazonia 1492: pristine forest or cultural parkland? *Science* **301**, 1710–1714. (doi:10.1126/science.1086112)
- Heckenberger, M. J., Peterson, J. B. & Neves, E. G. 1999 Village size and permanence in Amazonia: two archaeological examples from Brazil. *Latin Am. Antiquity* **10**, 353–376. (doi:10.2307/971962)
- Laurance, W. F. & Williamson, G. B. 2001 Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* **15**, 1529–1535.
- Laurance, W. F., Lovejoy, T., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. & Sampaio, E. 2002 Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* **16**, 605–618. (doi:10.1046/j.1523-1739.2002.01025.x)
- Lima, H. N., Schaefer, C. E. R., Mello, J. W. V., Gilkes, R. J. & Ker, J. C. 2002 Pedogenesis and pre-Colombian land use of "terra preta anthrosols" ("Indian black earth") of Western Amazonia. *Geoderma* **110**, 1–17. (doi:10.1016/S0016-7061(02)00141-6)
- Listopad, C. 2001 *Vegetational changes, fire history and human impact during the last 6000 years: a paleoecological study of the Madre de Dios Province, Lowland Peru*. Melbourne, FL: Florida Institute of Technology.
- Liu, K.-b. & Colinvaux, P. A. 1988 A 5200-year history of Amazon rain forest. *J. Biogeogr.* **15**, 231–248. (doi:10.2307/2845412)
- Mann, C. C. 2000 Earthmovers of the Amazon. *Science* **287**, 786–789. (doi:10.1126/science.287.5454.786)
- Matheny, R. T. & Gurr, D. L. 1983 Variation in prehistoric agricultural systems of the New World. *Annu. Rev. Anthropol.* **12**, 79–103. (doi:10.1146/annurev.an.12.100183.000455)
- Mayle, F. E. & Beerling, D. J. 2004 Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeogr. Palaeoclim. Palaeoecol.* **214**, 11–25. (doi:10.1016/j.palaeo.2004.06.016)
- Mayle, F. E., Burbridge, R. & Killeen, T. J. 2000 Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**, 2291–2294. (doi:10.1126/science.290.5500.2291)
- Meggers, B. J. 1954 Environmental limitation on the development of culture. *Am. Anthropol.* **56**, 801–824. (doi:10.1525/aa.1954.56.5.02a00060)
- Meggers, B. J. 1995 Judging the future by the past: the impact of environmental instability on prehistoric Amazonian populations. In *Indigenous peoples and the future of Amazonia: an ecological anthropology of an endangered world*, vol. 162 (ed. L. E. Sponsel), pp. 15–43. Tucson, AZ: University of Arizona Press.
- Meggers, B. J. 2003a Natural versus anthropogenic sources of Amazonian biodiversity: the continuing quest for El Dorado. In *How landscapes change* (eds G. A. Bradshaw & P. A. Marquet), pp. 89–107. Berlin, Germany: Springer.
- Meggers, B. J. 2003b Revisiting Amazonia circa 1492. *Science* **301**, 2067. (doi:10.1126/science.302.5653.2067b)
- Moy, C. M., Seltzer, G. O., Rodbell, D. T. & Anderson, D. M. 2002 Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* **420**, 162–164. (doi:10.1038/nature01194)
- Nepstad, D., Lefebvre, P., Lopes da Silva, U., Tomasella, J., Schlesinger, P., Solórzano, L., Moutinho, P., Ray, D. & Guerreira, B. J. 2004 Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Global Change Biol.* **10**, 704–717. (doi:10.1111/j.1529-8817.2003.00772.x)
- Paduano, G. M., Bush, M. B., Baker, P. A., Fritz, S. C. & Seltzer, G. O. 2003 A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. *Palaeogeogr. Palaeoclim. Palaeoecol.* **194**, 259–279. (doi:10.1016/S0031-0182(03)00281-5)
- Phillips, O. 1993 The potential for harvesting fruits in tropical rainforests: new data from Amazonian Peru. *Biodiversity Conserv.* **2**, 18–38.
- Piperno, D. R. 1990 Aboriginal agriculture and land usage in the Amazon Basin, Ecuador. *J. Archaeol. Sci.* **17**, 665–677.
- Piperno, D. R. & Becker, P. 1996 Vegetational history of a site in the Central Amazon basin derived from phytolith and charcoal records from natural soils. *Quatern. Res.* **45**, 202–209. (doi:10.1006/qres.1996.0020)
- Piperno, D. R. & Pearsall, D. M. 1998 *The origins of agriculture in the lowland neotropics*. San Diego, CA: Academic Press.
- Piperno, D. R., Bush, M. B. & Colinvaux, P. A. 1991 Paleoecological perspectives on human adaptation in Panama. II: the Holocene. *Geoarchaeology* **6**, 227–250.
- Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Nunez, P. V., Neill, D. A., Cerón, C. E., Palacios, W. E. & Aulestia, M. 2001 Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**, 2101–2117. (doi:10.2307/2680219)
- Prance, G. T. & Schubart, H. O. R. 1977 Nota preliminar sobre a origem das campinas abertas de areia branca do baixo Rio Negro. *Acta Amazonica* **7**, 567–570.
- Roosevelt, A. C. 1980 *Parmana: prehistoric maize and manioc subsistence along the Amazon and Orinoco*. New York, NY: Academic Press.
- Roosevelt, A. C. 1987 Chiefdoms in the Amazon and Orinoco. In *Chiefdoms in the Americas* (eds R. C. Drennen & C. A. Uribe), pp. 153–185. Lanham, MD: University Press of America.
- Roosevelt, A. C. 1991 *Moundbuilders of the Amazon: geophysical archaeology on Marajó Island, Brazil*. San Diego, CA: Academic Press.
- Roosevelt, A. C., Housley, R. A., Imazio da Silveira, M., Maranca, S. & Johnson, R. 1991 Eighth millennium pottery from a prehistoric shell midden in the Brazilian Amazon. *Science* **254**, 1621–1624. (doi:10.1126/science.254.5038.1621)
- Saldarriaga, J. G. & West, D. C. 1986 Holocene fires in the northern Amazon basin. *Quatern. Res.* **26**, 358–366. (doi:10.1016/0033-5894(86)90095-5)

- Sanford, R. L., Saldarriaga, J., Clark, K. E., Uhl, C. & Herrera, R. 1985 Amazon rainforest fires. *Science* **227**, 53–55.
- Santos, G. M., Gomes, P. R. S., Anjos, R. M., Cordeiro, R. C., Turcq, B. J., Sifeddine, A., di Tada, M. L., Cresswell, R. G. & Fifield, L. K. 2000  $^{14}\text{C}$  AMS dating of fires in the central Amazon rain forest. *Nucl. Instrum. Methods Phys. Res. B* **172**, 761–766.
- Servant, M., Fontes, J.-C., Rieu, M. & Saliège, X. 1981 Phases climatiques arides holocènes dans le sud-ouest de l'Amazonie (Bolivie). *C. R. Acad. Sci. Paris, Ser. II* **292**, 1295–1297.
- Silman, M. R., Terborgh, J. W. & Kiltie, R. A. 2003 Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* **84**, 431–438.
- Smith, N. J. H. 1980 Anthrosols and human carrying capacity in Amazonia. *Ann. Assoc. Am. Geogr.* **50**, 553–566. (doi:10.1111/j.1467-8306.1980.tb01332.x)
- Stockmarr, J. 1971 Tablets with spores used in absolute pollen analysis. *Pollen Spores* **13**, 615–621.
- Stuiver, M. & Reimer, P. J. 1993 Extended  $^{14}\text{C}$  database and revised CALIB radiocarbon calibration program. *Radiocarbon* **35**, 215–230.
- Turcq, B., Sifeddine, A., Martin, L., Absy, M. L., Soubles, F., Sugio, K. & Volkmer-Ribeiro, C. 1998 Amazonia rainforest fires: a lacustrine record of 7000 years. *Ambio* **27**, 139–142.
- Vickers, W. T. 1988 Game depletion hypothesis of Amazonian adaptation: data from a native community. *Science* **239**, 1521–1522. (doi:10.1126/science.3353699)
- Whitlock, C., Bradbury, J. P. & Millsbaugh, S. H. 1997 Controls on charcoal distribution in lake sediments: case studies from Yellowstone National Park and north-western Minnesota. In *Sediment records of biomass burning and global change* (eds J. S. Clark, H. Cachier, J. G. Goldammer & B. Stocks), pp. 367–386. Berlin, Germany: Springer.
- Whitlock, C. & Larsen, C. 2001 Charcoal as a fire proxy. In *Tracking environmental change using lake sediments*, vol. 3 (eds J. P. Smol, H. J. B. Birks & W. M. Last), *Terrestrial, algal and siliceous indicators*, pp. 75–98. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Wyatt, J. L. & Silman, M. R. 2004 Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia* **140**, 26–35.