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Anthropogenic Soils and Tree Distributions in a Lowland Forest in Bolivia

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ABSTRACT

The distributions of 17 tree species with seeds or fruits that are commonly eaten or otherwise used by humans were studied in reference to anthropogenic soils in a seasonally dry lowland tropical forest in Bolivia. Two types of anthropogenic dark earths (ADEs) were identified: terra preta (TP: darkened with charcoal fragments and with abundant pottery shards) and terra mulata (TM: somewhat darkened but with little or no pottery). In 216 ha, we compared the densities of trees > 10 cm dbh of useful species in nine TP patches, three TM patches, and six areas with nonanthropogenic soils (N-ADE). The TP, which covers approximately 20 percent of the sample area, has higher contents of organic matter, extractable P, and extractable Ca than N-ADE soils, as well as higher pH and extractable P than TM. TM has organic matter and Ca contents similar to N-ADE soils but significantly less extractable K. In general, TP has higher nutrient content than surrounding soils, both at the surface (0–10 cm) and deeper in the profile (40–50 cm). Despite these differences in soil fertility and contrary to our expectations, none of the 17 tree species were concentrated on TP perhaps because interactions between local dispersal agents and natural disturbances have masked historical patterns. Alternatively, past inhabitants of the study area may have enriched forests with useful tree species in areas where they were not practicing the intensive soil husbandry that results in ADEs.

Key words: Amazonian dark earths; forest history; terra preta.

Evidence is accumulating that humans dramatically influenced wide expanses of forests throughout the tropics (Willis *et al.* 2004). In the case of Amazonia, although pre-Colombian human populations and their environmental impacts are still being debated (Dobyns 1966; Denevan 1992a; Meggers 1995, 2003; Roosevelt 2003), it is commonly accepted that Amerindian populations declined by 90 percent within 100 yr after European contact (Hemming 1978). Furthermore, many Amazonian forests once considered pristine are now recognized as having regenerated after cessation of human activities (Lentz 2000, Heckenberger *et al.* 2007; but see Bush & Silman 2007). Human influences are to be expected, given that they have been present in Amazonia for at least 12,000 yr (Roosevelt *et al.* 1991). Pre-Columbian Amazonian societies affected the region in dramatic ways such as through construction of raised fields, earthen causeways, and hydraulic earthworks (Denevan 1966, Lippi 1988, Erickson 2000, Roosevelt 2000, Heckenberger *et al.* 2007), and also through the less obvious forest and soil management practices that are the focus of this study (Posey 1985, Balée 1994, Denevan 1998, Peters 2000).

While slash-and-burn agriculture with short cropping periods and long fallows is often considered the 'traditional' approach to farming on the generally nutrient-poor soils of Amazonia, recent insights from anthropologists and soil scientists raise questions about this assumption. In particular, the challenge of felling trees with stone axes (*e.g.*, Denevan 1992b; but see Jorgensen 1985) coupled with the widespread distribution of soils that reflect substantial and prolonged husbandry argue for more intensive farming practices. These anthropogenic dark earths (ADEs), referred to originally in Brazil and now elsewhere as terra preta or terra preta do índio, are nutrient-rich and occur in patches of 0.5–300 ha, typically embedded in a matrix of infertile soils (mainly oxisols and ultisols; for recent reviews see Lehmann *et al.* 2003, Glaser & Woods 2004). Abundant organic matter and elevated nutrient contents (especially phosphorus, calcium, potassium and sodium) distinguish ADEs from soils in their surroundings (Smith 1980, Woods *et al.* 2000, Glaser *et al.* 2001, McCann *et al.* 2001). By incorporating charcoal and wood ash, pre-Columbian farmers increased soil organic matter (SOM), nutrient retention, cation exchange capacity (CEC), and pH (Woods *et al.* 2000). Because charcoal persists in soil for millennia (Rainho Texeira *et al.* 2002), it contributes to the maintenance of anthropogenic soil properties long after soil husbandry ceases. The fertility of these soils was reportedly further enhanced with household wastes (*e.g.*, food remains, shells, bones, feces, blood, and urine), and other organic material brought from the surrounding forests (*e.g.*, palm leaves) and wetlands (*e.g.*, aquatic plants; Smith 1980, McCann *et al.* 2001). Initially, ADEs were discovered near floodplains, especially on river bluffs along the main Amazon River (Sombroek 1966, Smith 1980, Andrade 1986). More recently, large areas with ADEs have been reported in upland forests (Heckenberger *et al.* 1999) and in floodplains along tributaries of the Amazon (McCann *et al.* 2001). In any case, most of the reported occurrences of ADEs in South America to date are near permanent sources of water.

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Two kinds of ADEs, terra preta (TP) and terra mulata (TM), have been described as being clearly distinguishable in Brazil (Sombroek *et al.* 2002). TP appears in former human settlements and, besides being enriched in nutrients and charcoal, contains abundant pottery and other cultural debris (Smith 1980, Heckenberger *et al.* 1999). TM is thought to have developed in permanent agricultural fields that were enriched by long-term soil-management practices such as mulching and infield burning (Denevan 1996, Woods *et al.* 2000, McCann *et al.* 2001). ADE creation apparently ceased centuries ago, and despite some recent advances, the nature and characteristics of the agricultural practices that resulted in its formation of ADEs remain poorly understood.

High nutrient levels of ADEs and associated management practices are expected to influence the vegetation that either persists or colonizes ADE sites after their abandonment. In particular, near-settlement enrichment of native plant communities with species used by humans likely occurred before as well as after the advent of agriculture. For example, hunters and gatherers probably selected and favored certain plant species both purposefully by planting and inadvertently by consuming fruits and disposing of seeds in or near their settlements (Smith 1995, Peters 2000). In Amazonia, fruits were harvested by humans and their seeds transported since at least 10,500 yr BP (Roosevelt *et al.* 1996). The alteration of forests and landscapes was even more dramatic after development of intensive agricultural systems, such as maize cultivation, which developed in the tropical lowlands of the Americas 6000–7000 yr BP (Bush *et al.* 1989, Pearsall 1992, Piperno & Pearsall 1998).

Many common canopy tree species in Bolivia regenerate poorly even after the overstory is opened by selective logging (Mostacedo & Fredericksen 1999). In contrast, these same species regenerate abundantly in heavily disturbed areas such as along logging roads, in large logging gaps with surface soils disturbed by harvesting equipment (Fredericksen & Mostacedo 2000, Fredericksen & Pariona 2002), and in abandoned agricultural clearings (Kennard 2002, Peña-Claros 2003, Peña-Claros *et al.* 2008). Past land-use practices by indigenous people such as large-scale clearing and frequent burning presumably provided conditions suitable for recruitment by these species, several of which may also have been cultivated (*e.g.*, *Spondias mombin* and *Sapindus saponaria*). We expected other species with edible or otherwise useful seeds or fruits to have been intentionally or inadvertently planted very frequently near dwellings (Balée 1994, Smith 1995, Lamont *et al.* 1999). In particular, multiple-use palms are often found in abundance near present-day indigenous villages and abandoned village sites (Brücher 1989, Clark *et al.* 1995, Henderson 1995, Moraes-Ramirez 1996, Morcote-Rios & Bernal 2001).

This study examines the influence of historical Native American land-use practices on soils and on tree species distributions in a seasonally dry 'transitional' forest in lowland Bolivia. We focus on tree species with seeds or fruits that we expect were eaten or otherwise used by the people that lived in the study site before its abandonment. We compare the chemical properties of anthropogenic and nonanthropogenic soils and then test the hypothesis that useful tree species are concentrated on the former.

METHODS

STUDY SITE.—This study was conducted in the 100,000-ha timber concession of Agroindustria Forestal La Chonta Ltda. (hereafter La Chonta), a lowland tropical forest in Guarayos Province, Department of Santa Cruz, Bolivia (15°45′ S, 62°60′ W; Fig. 1). The annual mean precipitation is *ca* 1500 mm with a severe dry season between May to October; the mean annual temperature of 24.3°C. The concession was very lightly selectively logged ($< 1\ m^3$/ha) for mahogany (*Swietenia macrophylla*) and tropical cedar (*Cedrela odorata*) during the 1970s. When these precious woods were depleted, the focus shifted to the 12–14 species being harvested at the time of this study (2000–2001). Our study was carried out in plots established as part of a long-term silvicultural research project managed by the Instituto Boliviano de Investigaciones Forestales (IBIF; Putz *et al.* 2004, Blate 2005, Peña-Claros *et al.* 2008).

The vegetation of La Chonta is classified as subtropical humid forest (Holdridge 1971); common tree species include *Pseudolmedia laevis*, *Ocotea guianensis*, *Clarisia racemosa*, *Terminalia oblonga*, and *Hura crepitans* (Fredericksen & Pariona 2002, Navarro & Maldonado 2002). The canopy is semideciduous and fairly open, with mature forest heights of 20–25 m. Lianas are remarkably abundant in the forest (Alvira *et al.* 2004). The area has a long history of both human-induced and 'natural' fires, but there were no signs of recent fires in our study area. Based on annual ring counts on the stumps of harvested *Hura crepitans* (N = 5) and *Cariniana ianeirensis* (N = 5) trees, many canopy trees in the forest are at least 140 yr old. La Chonta has numerous ephemeral streams and the rivers Blanco and Negro border the concession, but the nearest permanent source of surface water is about 14 km from the study site (Fig. 1).

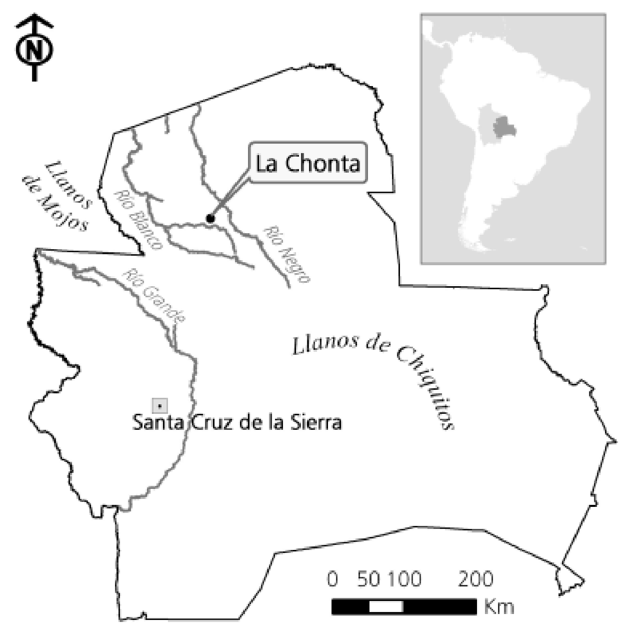

FIGURE 1. Location of the study site in lowland Bolivia.

SOIL SAMPLING AND ANALYSIS.—An area of 216 ha was surveyed for anthropogenic soils along trails separated by 150 m. Surface soil was examined at 200-m intervals for the dramatic darkening characteristic of ADEs; when it darkened markedly, sampling intervals were reduced to 100 m and soils were examined more thoroughly for charcoal and pottery.

Soil was classified as TP when extremely dark in color (Munsell System; 7.5 YR 3/1 and 2.5/1; dark brown and very dark brown) and both charcoal and pottery sherds were present. Soil that was somewhat darkened (7.5 YR 4/3–3/2, brown to dark brown), but had little or no pottery was classified as TM. Soils with no apparent indicators of anthropogenic influences were classified as non-Amazonian dark earth (N-ADE), most of which are ultisols (Navarro & Maldonado 2002). When TP was encountered, the area with this distinctive soil was estimated by sampling in the four cardinal directions every 20 m with a soil auger until the patch limits were identified. Soil samples 0–10 and 40–50 cm depth were taken from the corners of a 10×10 m square in center of each TP and adjacent area of TM, and from the surrounding N-ADE soils. Samples from each depth were mixed and 200 g of each was air dried and stored for laboratory analysis. In the laboratory, SOM was estimated using the weight loss on ignition method (Nelson 1996). Total phosphorus (P) was measured colorimetrically after sulfuric acid digestion (Olsen & Sommers 1982). Extractable phosphorous was measured colorimetrically after treatment with a Mehlich double-acid solution (Olsen & Sommers 1982). Finally, extractable calcium (Ca), magnesium (Mg), and potassium (K) were assayed using atomic absorption following extraction in a Mehlich double-acid solution (Thomas 1982). To compare soil types, the chemical data were analyzed with a two-way ANOVA model using soil type (TP, TM, and N-ADE) and depth as factors and sites as replicates.

As a preliminary archaeological assessment, one test pit (1×1 m^3) was excavated in the central of each of nine TP patches to quantify the abundance of pottery sherds and to determine the depth of the anthropogenic horizon. Two large charcoal fragments found intermixed with pottery sherds near the top of the TP layer (10 and 20 cm, respectively) were submitted to Beta Analytic Laboratory for accelerator mass spectrometry (AMS) radio-carbon dating.

SPECIES SELECTION.—Based on a preliminary floristic inventory coupled with a literature search, 17 tree species with fruits eaten or otherwise used by humans were selected for study (Table 1). Several of these species are reportedly semi-domesticated or domesticated by tropical South American indigenous groups (Clement 1986, 1999; Smith *et al.* 1992; Balée 1994; Henderson 1995) and all are presently used by indigenous peoples in lowland Bolivia (Centurión & Krajlevic 1996, Vásquez & Coimbra 1996, DeWalt *et al.* 1999, Mostacedo & Uslar 1999, Paz *et al.* 2001). All of the species studied regenerate at least sparsely in the forest, with the exception of *Bactris gasipaes*, which has not been observed as seedlings in La Chonta but is widely cultivated (Killeen *et al.* 1993, Postma & Verheij 1994, Clement 1999, Morcote-Rios & Bernal 2001).

Information about uses and regeneration status was gathered for each tree species through field observations, interviews with local foresters, and available literature (Table S1). Geographical distributions are based on the Missouri and New York Botanical Garden databases (Solomon 2002, New York Botanical Garden 2003). Maximum stem diameters and growth rates are derived from unpublished databases from IBIF (Table S1).

PLANT SPECIES SAMPLING.—Densities of each of the selected species were recorded in 50×20 m plots in separate areas of each of the three soil types. Plots were established in 14 TP sites, 10 adjacent TM sites, and 14 surrounding areas of N-ADE soils. TP patches ranged from 0.3 to 10.0 ha; we did not determine the sizes of the patches of TM soil, all of which were found adjacent to TP; both TP and TM were found in a matrix of N-ADE soils. One to three plots were established in 0.1–0.5 ha TP patches and five plots were established in patches > 0.5 ha, but patches were treated as replicates; TM and N-ADE areas were both sampled with five plots each with no plots < 200 m apart.

RESULTS

AREA, SHAPE AND LOCATION OF ANTHROPOGENIC SOIL PATCHES.—In an area of 216 ha, nine patches of TP (Supporting Table S2), three patches of TM, and six nearby (within 1 km) areas of N-ADE soil were identified. The TP patches were commonly located on flat terraces within 200 m of intermittent streams (Fig. 1). TP patch sizes varied in size and shape with many small circular patches (0.3–2.5 ha) and a few larger, irregular patches (5–10 ha; TP patch sizes and locations listed in Table S1). Within the TP sites, we found small areas with particularly high concentrations of charcoal and pottery sherds, perhaps corresponding to kitchen middens. The cumulative area of TP accounts for *ca* 20 percent of the study area (Table S2). TM patches were 0.3–1.0 ha and tended to surround the TP sites. We did not measure all the TM patches but estimate them to cover at least an additional 5 percent of the 216 ha study area.

Preliminary archaeological investigations carried out in pits excavated in TP revealed easily distinguished layers, defined by different densities of pottery sherds and charcoal. In all TP patches the surface 10 cm was dark in color but usually contained no pottery or large pieces of charcoal (except where recently disturbed by animals or road building activity). TP in patches < 1 ha generally had one continuous stratum of dark soil with evenly distributed pottery sherds and large pieces of charcoal from 10 cm down to 30–45 cm. In contrast, TP in the larger patches generally had two separate layers with pronounced anthropogenic influences, one at 10–40 cm and another at 45–75 cm; a 4–6-cm-thick layer of sandy-loam with large quartz crystals separated the two dark layers.

The density of buried pottery sherds in the intensively inventoried soil pits in TP varied from 19 to 187 pieces/m^3. We also found solid pieces of macroscopic black carbon (1–5 cm diam.) at 10–75 cm soil depth in both the small and large patches of TP. The two charcoal fragments found mixed with pottery in *TP* site 3 at 10 and 20 cm below the surface were AMS dated from 330 ± 80 to 420 ± 60 yr BP, respectively.

TABLE 1. *Characteristics of tree species that are commonly used by humans and that were selected for study in La Chonta.*

Family	Species	Local name	Uses	Growth Form	Geographical distribution	Regeneration status[a]
Anacardiaceae	*Spondias mombin*[b]	Ocorocillo	Edible fruits, medicinal bark	Emergent	Mexico to Bolivia	Poor
Arecaceae	*Astrocaryum aculeatum*[b]	Chonta de anillo	Edible fruits and seeds, oil, construction	Subcanopy	Amazonia	Poor
Arecaceae	*Astrocaryum murumuru*	Chonta	Edible fruits and seeds, oil, construction	Canopy	Amazonia	Medium
Arecaceae	*Attalea phalerata*	Motacú	Edible fruits and seeds, medicine, construction	Canopy	SW Amazonia	Good
Arecaceae	*Bactris gasipaes*[c]	Chonta	Edible fruits, medicine, bows, construction	Canopy	Central America to Bolivia.	Poor
Arecaceae	*Syagrus sancona*	Sumuqué	Construction, fruits and seeds used to attract game	Emergent	Amazonia	Medium
Bombacaceae	*Ceiba pentandra*	Hoja de yuca	Religious, fiber, oil from seeds	Emergent	Pantropical	Poor
Leguminosae (Mimosoideae)	*Inga* spp.[b]	Pacay	Edible fruit; *Inga edulis* cultivated	Subcanopy, pioneer	Pantropical	Good
Moraceae	*Batocarpus amazonicus*	Mururé	Edible fruits, dye, latex	Canopy	Panama to Bolivia	Poor
Moraceae	*Pourouma cecropiaefolia*	Uvilla	Edible fruits, medicinal	Canopy, pioneer	Costa Rica to Bolivia	Good
Myrtaceae	*Eugenia* sp.[b]	Arrayán	Edible fruits	Subcanopy	Pantropical	Good
Myrtaceae	*Myrcia* sp.	Sawinto	Edible fruits	Canopy	Amazonia	Poor
Sapindaceae	*Sapindus saponaria*	Isotouvo	Soap from fruits, medicinal	Subcanopy	Arizona to Bolivia	Good
Sapindaceae	*Talisia sculenta*	Pitón	Edible fruits	Subcanopy	Amazonia	Poor
Sapotaceae	*Pouteria macrophylla*[b]	Lúcma	Edible fruits	Canopy	Amazonia	Good
Sapotaceae	*Pouteria nemorosa*	Coquino	Edible fruits	Canopy	Disjunct, Ecuador and Bolivia	Good
Ulmaceae	*Ampelocera ruizii*	Blanquillo	Edible fruits	Canopy	Amazonia	Good

[a]Good: seedlings, saplings (< 1.5 m), juveniles (> 1.5 m) and adults present in the forest; Medium: juveniles and adults present, regeneration scarce; Poor: only adults present, regeneration scarce. This classification is valid only for La Chonta.

[b]Semi-domesticated.

[c]Domesticated according to Clement (1999).

SOIL CHEMISTRY.—Soils of La Chonta were all high in pH, averaging 7.2 in the TP, 6.4 in the TM, and 7.2 in the N-ADE soils (Table 2); TP and N-ADE soil pHs were significantly higher than in the TM ($P < 0.006$; Fig. 2A). Organic matter content at 10 and 50 cm depth averaged, respectively, 5.7 and 2.6 percent in TP, 4.8 and 2.1 percent in TM, and 4.7 and 2.1 percent in N-ADE soils; organic matter contents were significantly higher in the TP than in the N-ADE soils ($P < 0.039$; Table 3). Total P was consistently high and not significantly different among the three soil types (Table 3). Extractable P, in contrast, was significantly higher in TP than TM at both depths and significantly higher in TP than N-ADE soils at 50 cm ($P < 0.015$; Fig. 2C). Extractable Ca was extremely high in all La Chonta soils but was significantly higher in TP than TM or N-ADE soils ($P < 0.002$; Fig. 2D). Extractable K was significantly higher in TP and N-ADE soils than in TM ($P < 0.015$; Fig. 2E).

All of the soil properties tested, with the exception of pH and total P, were significantly higher at 10 cm than at 50 cm depth (Table 3). Organic matter content, extractable P and extractable Ca were significantly higher in TP than TM and N-ADE at 50 cm depth (Fig. 2B–D). Overall, the transitional TM soils had lower nutrient concentrations than N-ADE soils.

VEGETATION.—Contrary to our expectations, the densities of the 17 tree species studied did not differ significantly among the three soil types, (Fig. 3) but there were trends that might indicate soil preferences or historical effects. Although the differences were not significant, presumably due to high variances, six species (*Inga* spp., *S. mombin, Astrocaryum aculeatum, B. gasipaes*, *Ceiba pentandra*, and *Pouteria nemorosa*) were slightly more abundant in TM areas and *P. macrophylla* was slightly more abundant in N-ADE soils when compared with TM and TP.

When analyzing the differences between the ADEs and non-anthropogenic soils, the only species showing significant differences was *P. macrophylla*, which was more abundant in N-ADE soils than

TABLE 2. *Mean values (± 1 SE) of terra preta, terra mulata, and non-anthropogenic dark earth soil properties at two depths (0–10 and 40–50 cm) with sites as replicates. Total P was measured colorimetrically after sulfuric acid digestion. Extractable P was measured colorimetrically, and Ca, Mg and K were measured and using atomic absorption after a Mehlich double-acid extraction.*

	Terra preta ($N = 10$)		*Terra mulata* ($N = 3$)		Non-anthropogenic dark earth ($N = 6$)	
Soil property	0–10 cm	40–50 cm	0–10 cm	40–50 cm	0–10 cm	40–50 cm
pH (in water)	7.3 ± 0.1	7.2 ± 0.1	6.6 ± 0.3	6.3 ± 0.3	7.3 ± 0.3	7.0 ± 0.2
% Organic matter	5.7 ± 0.4	2.6 ± 0.2	4.8 ± 0.8	2.1 ± 0.3	4.7 ± 0.3	2.1 ± 0.2
C/N ratio	10.8 ± 0.6	12.0 ± 0.6	10.2 ± 0.3	11.9 ± 0.17	10.1 ± 0.2	12.1 ± 0.3
Total P (μg/g)	203 ± 34	322 ± 41	171 ± 30	166 ± 54	155 ± 22.3	358 ± 88
Extractable P (mg/kg)	49.7 ± 16.4	35.9 ± 17.7	6.66 ± 1.44	2.84 ± 0.82	26.0 ± 9.8	4.34 ± 1.07
Extractable K (mg/kg)	94.4 ± 8.2	62.5 ± 7.9	57.0 ± 9.6	28.4 ± 6.4	91.8 ± 13.0	55.2 ± 8.9
Extractable Ca (mg/kg)	3180 ± 289	1429 ± 115	1976 ± 329	587 ± 162	2435 ± 334	805 ± 144
Extractable Mg (mg/kg)	87.0 ± 14.7	35.5 ± 3.8	58.2 ± 1.4	40.8 ± 7.2	60.1 ± 3.7	31.6 ± 5.8

in ADE areas (Mann–Whitney $U = 254$, $P = 0.009$, df = 1; Fig. 3O). *Astrocaryum aculeatum* and *C. pentandra* were rare but were only recorded in TP and TM areas (Fig. 3B and G).

DISCUSSION

AREA, SHAPE AND LOCATION OF ANTHROPOGENIC SOIL PATCHES.—In contrast to the majority of anthropogenic dark earth areas in the Amazon Basin (Sombroek 1966, Smith 1980; for recent reviews see Lehmann *et al.* 2003, Glaser & Woods 2004), the anthropogenic soils of La Chonta are far from permanent water sources. In fact, researchers and logging crews truck in barrels of water to their camps during the dry season. The closest rivers, Ríos Negro and Blanco, are 14–30 km from the TP areas we studied (Fig. 1) and flow in the small streams that run through the area ceases completely during the late dry season (May–October). In contrast, TP in the Brazilian Amazon is mostly associated with large rivers (Smith 1980, Roosevelt 1989, McCann *et al.* 2001) but a large TP site (200 ha) 15 km from the Amazon River was described by Smith (1999). Perhaps the river courses or stream flows in La Chonta have changed since the time when the ADEs were created, or the prehistoric residents constructed wells or dams of which we are unaware.

The processes of community settlement, abandonment, and reoccupation may help explain the observed variation in TP patch size. On the basis of the presence of two anthropogenic soil layers, we propose that the larger patches (5–10 ha) were occupied more than once. If this is true, then the size of these large patches may be an inaccurate indicator of village size, as suggested by Meggers (1995) for TP areas in Brazil. Nevertheless, more archaeological research is needed to determine precisely the land-use practices used in the large areas of TP and TM.

The two C-14 dates for charcoal that was mixed with pottery at 10 and 20 cm depth suggest that at least one of the sites (TP Site 3) was inhabited 300–400 BP, but provide no indication of the prior duration of settlement. Given that charcoal and pottery are present deeper in the soil (to 75 cm) in other TP sites, more soil charcoal C-14 dates are needed to establish the sequence of human occupation of La Chonta.

In La Chonta we found charcoal at greater depths (75 cm) than reported by Glaser *et al.* (2000) in Brazil (30–40 cm), but charcoal, presumed to be from wildfires, is commonly reported to 1 m depths in neotropical forests soils (Saldarriaga *et al.* 1988, Horn & Sanford 1992, Hammond *et al.* 2007). The presence of charcoal and pottery sherds deep in the soil could also result from bioturbation by giant armadillos and other animals. Finally, TM in Brazil is described as covering large areas in which TP sites are embedded (Sombroek *et al.* 2002), whereas in La Chonta, our preliminary surveys suggest that TM areas are smaller and occur only as narrow bands around TP patches. Further mapping of ADEs in La Chonta would clarify these spatial relationships and facilitate comparisons with other sites.

SOIL CHEMISTRY.—Perhaps the main difference between the ADEs of La Chonta and those described from other parts of the Amazon Basin is the type of soils from which they were derived. In contrast to most Amazonian soils, La Chonta soils have circum-neutral pH. Therefore, even though reported pH values in Brazilian ADEs (4.8–5.5; Smith 1980, Glaser *et al.* 2000, Sombroek *et al.* 2002) are higher than their surrounding soils (generally < 4.8), they are much more acidic than any of the soils of La Chonta. The pHs of ADEs of La Chonta were not significantly different from the N-ADE soils, which was also reported by Eden *et al.* (1984) for much more acidic TP and surrounding soils in Caquetá, Colombia (pH 4.3–4.8 for TP and 4.0–4.5 for surrounding inceptisols).

SOM concentrations at La Chonta were significantly higher in TP than in the surrounding soils, corresponding with the results of research in the Brazilian Amazon (Smith 1980, Glaser *et al.* 2000, Sombroek *et al.* 2002). In La Chonta, in contrast, concentrations of organic matter did not differ between TM and TP, whereas Brazilian TM often has more organic matter than TP (Woods & McCann 1999, McCann *et al.* 2001, Sombroek *et al.* 2002).

Although total P is considered a good indicator of former human occupation (*e.g.*, Eidt 1977), total P did not differ between TP, TM, and N-ADE soils in La Chonta. In contrast to the results for total P, extractable P differed among the three soil types in La Chonta, being higher in TP than TM and N-ADE soils.

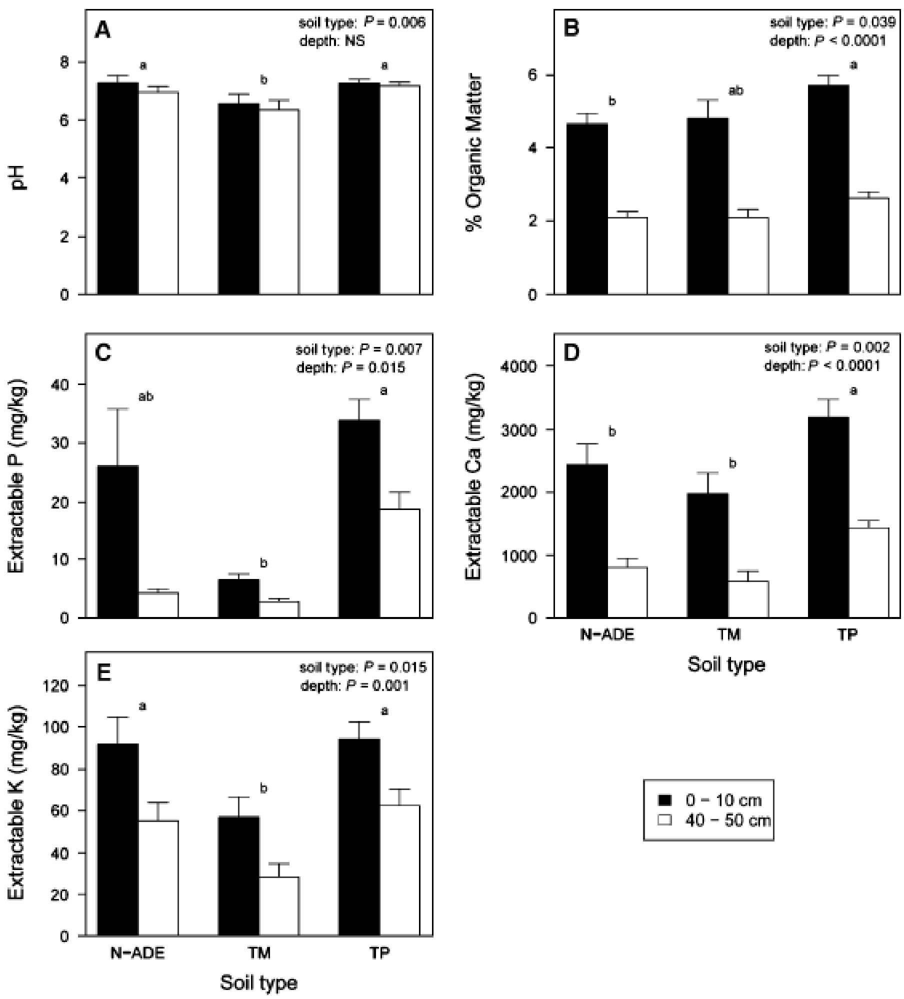

FIGURE 2. Mean values (+SE) for terra preta (TP, $N=10$), terra mulata (TM, $N=3$,), and non-anthropogenic dark earth (N-ADE, $N=6$) at two different depths. (A) pH; (B) Organic matter content; (C) Extractable phosphorous; (D) Extractable calcium; (E) extractable potassium. Different letters indicate overall significant differences among means of the three soil types.

Nevertheless, the amounts of extractable P in La Chonta's TP (50 and 36 mg/kg at 10 and 50 cm, respectively) were much lower than reported for TP in Brazil (358 and 619 mg/kg at 30 cm, Heckenberger *et al.* 1999; 175 mg/kg at 20 cm, Smith 1980; and 600 mg/kg, Woods & McCann 1999). While P is limiting in most tropical soils, occurring typically at < 6 mg/kg (Kellman & Tackaberry 1997, McGrath *et al.* 2001, Fardeau & Zapata 2002), its presence at higher concentrations in TP, particularly deep in the soil, positively influences its fertility. Not surprisingly, TP is currently valued in Brazil as agricultural sites and sold to suburbanites by the truckload for gardening (Smith 1980).

TM has been reported as having slightly higher extractable P content than the surrounding nonanthropogenic soils in Brazil (McCann *et al.* 2001, Sombroek *et al.* 2002), but in La Chonta, TM soils had the same (at 50 cm) and less (at 10 cm) extractable P than N-ADE soils. One possible explanation for the relative lack of nutrients (particularly P and Ca) in TM soils may be that former inhabitants of La Chonta removed nutrients from TM areas when they moved plant material to TP areas to use as green manure or for 'infield burning'. Certainly, the removal of plant material can locally diminish nutrients (*e.g.*, Glatzel 1991). Additional studies in TM soils in La Chonta are necessary to test this hypothesis.

The high levels of Ca in the TP of La Chonta resemble those found by Heckenberger *et al.* (1999) near the Negro and Xingu rivers in the Brazilian Amazon. These high concentrations can be explained by additions of bones, shells, and ash (Smith 1980, McCann *et al.* 2001). In La Chonta, although significantly lower than in TP, extractable Ca was still very high for TM and N-ADE soils. These results can be explained by the nature of the parent material combined with anthropogenic influences that might have affected ADE as well as N-ADE soil areas.

VEGETATION.—Our results showed few differences in the abundances of the 17 useful tree species on anthropogenic and nonanthropogenic soils in La Chonta. This unexpected result may be due to our misunderstanding of past land-use practices, but contemporary disturbances

TABLE 3. *Statistical contrasts of the three soil types (terra preta, terra mulata and non-anthropogenic dark earth) at two depths (0–10 cm and 40–50 cm).*

	Soils			Depth			Soils × Depth		
Soil property	df	F	P-value	df	F	P-value	df	F	P-value
pH (in water)	2	6.03	0.006	1	1.30	0.26	2	0.23	0.80
% Organic matter	2	3.60	0.039	1	72.9	< 0.0001	2	0.37	0.70
C/N ratio	2	0.21	0.81	1	8.63	0.006	2	0.24	0.79
Total P (ug/g)	2	1.55	0.23	1	5.81	0.022	2	1.53	0.23
Extractable P (mg/kg)	2	5.81	0.007	1	6.73	0.015	2	0.79	0.46
Extractable K (mg/kg)	2	4.83	0.015	1	12.6	0.001	2	0.06	0.94
Extractable Ca (mg/kg)	2	7.71	0.002	1	45.1	< 0.0001	2	0.18	0.83
Extractable Mg (mg/kg)	2	1.41	0.26	1	11.4	0.002	2	1.30	0.29

also need to be considered. It seems likely, for example, that former inhabitants of La Chonta altered the forest beyond the TP areas, influencing both TM and N-ADE soil areas. This would be the case if TP sites were villages and surrounding areas (TM and N-ADE soil areas) were managed forest or agricultural plots. Alternatively, a former concentration of useful tree species in TP and TM areas may have been masked by modern disturbances, natural dispersal, and other factors.

The six species that were slightly but not significantly more abundant on TM soils than TP and N-ADE soils may have once been concentrated if the TP areas were village sites mostly devoid of vegetation, and the TM sites were the surrounding agricultural plots. Four of the six species that tend to be more abundant in TM areas (*S. mombin, A. aculeatum, B. gasipaes* and *C. pentandra*) are present at overall low densities (0.21, 0.04, 0.02, and 0.05 trees/ha, respectively), are widely distributed long-lived species, and regenerate poorly in La Chonta (Table S1). In addition, they are all known to be cultivated near human settlements elsewhere in the tropics (particularly *B. gasipaes*; Brücher 1989, Smith *et al.* 1992, Clement 1999). It is possible, therefore, that they were planted by the people who lived in La Chonta as recently as 300–400 yr ago, but further studies at a larger scales will be necessary to test this hypothesis.

While palm distributions are influenced by a variety of environmental factors (*e.g.*, Anderson *et al.* 1991, McPherson & Williams 1998), they are commonly associated with human settlements (Clement 1999, Morcote-Rios & Bernal 2001). There are several reasons to expect that the *B. gasipaes* population of La Chonta is a relict of ancient cultivation. Despite maximum age estimates of 50–100 yr for each mature stem (Brücher 1989, Smith *et al.* 1992, Mora-Urpí *et al.* 1997), clones can live for centuries, perhaps since being planted by former inhabitants. In addition, *B. gasipaes* is the only species we studied that is considered fully domesticated (Clement 1999) and that does not regenerate naturally in La Chonta. However, several authors (Clement 1986, 1999; Mora-Urpí *et al.* 1997) recognize that there are different varieties of *B. gasipaes*, comprising a continuum between domesticated and semi-domesticated. In La Chonta, further studies of seed/fruit ratios will determine where *B. gasipaes* falls on this continuum. Similar to *B. gasipaes*, the small population of the semi-domesticated palm, *A. aculeatum* (Clement 1999), may also be a relict from earlier plantings given that it is often associated with human settlements (Wessels Boer 1965) and regenerates poorly in La Chonta. The fact that *B. gasipaes* and *A. aculeatum* are not significantly concentrated on the ADEs suggests in the past their management was not restricted to ADE sites.

Trees of short-lived species (< 100 yr) could not have been planted by former inhabitants of La Chonta because the area was abandoned > 140 yr ago, based on the ages of the oldest trees on which annual rings were counted, or > 330 yr ago, based on the youngest carbon date on charcoal near the top of the TP layer. For example, the maximum age of *Inga* spp. in La Chonta is estimated to be 117 yr. While several species of *Inga* are considered semi-domesticated, in particular *I. edulis* (Clement 1999), they are also dispersed by monkeys (Andresen 1999) and regenerate well in La Chonta (Table 2). Consequently, the apparent concentration of *Inga* spp. on TM soils (Fig. 3H) may be the product of a secondary ecological adaptation rather than the result of enrichment by past inhabitants of La Chonta.

The species with abundant regeneration, overall high densities, and no apparent pattern of concentration according to soil type, such as *Ampelocera ruizii* and *S. saponaria*, may be wild species that are used by people, but past uses apparently have not altered their present distribution in La Chonta. *Ampelocera ruizii* is not reported as domesticated or semi-domesticated in the literature and has a fairly narrow distribution, growing only in Brazil and the Bolivian lowlands (Table 1). In contrast, *S. saponaria* is considered to be native from Bolivia to Colorado, and is reported to be used by numerous indigenous groups (Brücher 1989). If the range of *S. saponaria* was expanded by humans, its regeneration status and distribution suggest that it has become wild in La Chonta.

The lack of apparent differences in the abundances of most of the species we studied on the different soil types may be explained by numerous interacting factors known to determine forest composition (*e.g.*, topography, physiography, land use history) as well as stochastic forces (Hubbell & Foster 1986). Certainly, edaphic and historic factors alone are not enough to explain forest composition in La Chonta, but their interactions with several other factors might do so. Clark *et al.* (1999), for example, determined that the distributions of only 30 percent of the species they studied in a lowland forest in Costa Rica were correlated with edaphic conditions and concluded that only mesoscale vegetation and soil sampling will estimate the true degree of edaphically influenced distributions. A larger scale study in La Chonta and its surroundings, integrating other environmental variables into the analysis, would allow us to do the same.

One of the main factors influencing the results of this study might be the extended period post-abandonment forest dynamics in the area. The two C-14 dates of charcoal suggest that the site was inhabited most recently 380 and 430 yr BP. This extended time since abandonment might be sufficient to mask the effects of humans' enrichment with useful species in the anthropogenic soil areas. In this time period, two or three generations of the short-lived trees can have developed and biotic and abiotic seed dispersal processes may have extended the species' distribution range beyond the

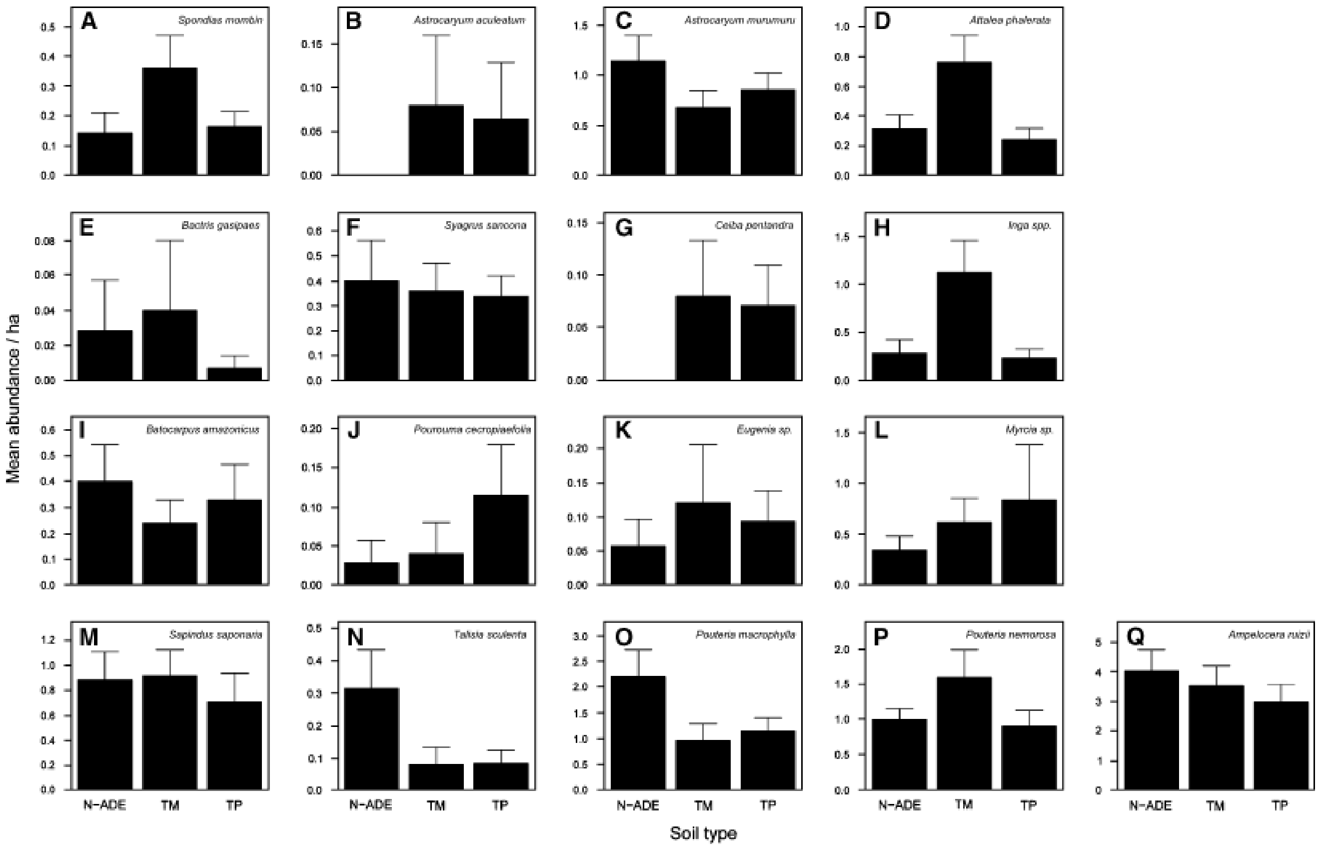

FIGURE 3. Comparisons of the relative abundances (± SE) of the selected useful tree species the on three different soil types: non-Amazonian dark earth (N-ADE, $N = 14$), terra mulata (TM, $N = 10$), and terra preta (TP, $N = 14$).

TP patches, if they were indeed initially concentrated there. In addition, disturbances such as fires and tree falls may have played a role in the distribution of useful species.

Although it is currently difficult to envisage 5–10 ha towns so far from permanent water sources, it is possible that the large TP areas in La Chonta were cleared and settled areas as they are and were in Amazonian Brazil (Heckenberger *et al.* 1999). If village sites were maintained clear of vegetation with a large central plaza and compacted soils (Woods *et al.* 2000), it is likely that the perimeter of these areas (TM and N-ADE sites) represent the agricultural zone that was enriched with useful species. If this is true in La Chonta, the soils surrounding TP sites are those more affected by past agricultural practices and are areas where useful species would have been managed or cultivated. Consequently, areas adjacent to ADE sites might not constitute a good control for testing the influence of past land-use practices on species composition. A better control area would be a similar forest without a history of human disturbances, which will be difficult to find.

The results of this study suggest that short-lived species with good regeneration and no pattern of concentration in anthropogenic soils, while perhaps used by former inhabitants, are now wild species that do not reflect the influence of past human use. In contrast, large individuals of long-lived species with poor regeneration may in fact be remnants of former cultivation. The lack of significant concentrations of useful species on ADEs suggests that species may have been cultivated or managed in adjacent non-ADE areas, that plant communities on all sites were influenced by human activities, or that over the centuries since the sites were abandoned, natural processes have obscured the anthropogenic patterns of tree distribution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Maximum diameters, mean growth rates for trees > 10 cm dbh, and abundances of the selected tree species in La Chonta.*

TABLE S2. *Distribution of terra preta sites in a 216 ha sample area.*

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