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A Late Holocene Pollen and Charcoal Record from La Selva Biological Station, Costa Rica

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ABSTRACT

Pollen and charcoal analysis of a 5.9-m-long sediment profile from a swamp on an alluvial terrace on the edge of La Selva biological station, Costa Rica (10°26′23″ N, 84°00′24″ W, 36 m asl), documents three millennia of human and natural disturbance within a lowland tropical rain forest. The record indicates that the highly diverse rain forest that presently surrounds the Cantarrana swamp regrew following forest clearing and maize agriculture that ended only a few centuries ago. The first maize pollen appears in sediments deposited ~1070 calendar-year BP. Older sediments below the 'maize zone' contain macroscopic charcoal, abundant microscopic charcoal, and possible pollen indicators of forest clearance, perhaps signaling local cultivation of root crops that left no pollen in the sediments. Interpretation of local archaeology indicates that La Selva reserve may have been most heavily populated during the El Bosque and La Selva regional archaeological phases from 2250–950 yr BP. However, the distribution of maize pollen in the sediments is clear evidence that the reserve was also occupied during the later La Cabaña phase (950–400 yr BP), from which few artifacts have yet surfaced. Natural forest disturbance from treefalls and stream dynamics, and hydrological shifts associated with late-Holocene climate variability, form a backdrop to the human land-use history preserved in the Cantarrana sediment profile.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: archaeology; disturbance; maize; paleoecology; pollen analysis; prehistoric agriculture; tropical rain forest; *Zea mays*.

Tropical forests worldwide have been subjected to a long history of human disturbance associated with agriculture, fires, hunting, and the gathering of wild plant resources. Natural disturbances such as treefalls, floods, droughts, and lightning-induced fires have also affected tropical forests at frequencies influenced by short-term climate events such as El Niño-Southern Oscillation, and by longer-term shifts in climate. Climate history has also influenced the nature of human activity within tropical forests. Information on past environmental conditions and the specific disturbance histories that have shaped modern forests at tropical research sites provides an important context for ecological and taxonomic research (Hamburg & Sanford 1986).

This paper reports evidence of prehistoric agriculture, fires, other forest disturbances, and climatic variability, preserved in a 5.9-m sediment core recovered from the Cantarrana (Singing frog) swamp on the edge of La Selva biological station in the Caribbean lowlands of Costa Rica (McDade *et al.* 1994). Biological research at this tropical rain forest research site began before archaeologists had surveyed the reserve, and early publications accordingly described mature forests as undisturbed by humans (Frankie *et al.* 1974, Hartshorn 1983a). Subsequent discoveries of pre-Columbian pottery, stone artifacts, and remains of structures established that prehistoric people occupied alluvial terraces at La Selva by at least 3000 yr BP (Sol 2000). These findings from the fertile terraces along major streams bordering La Selva sparked interest in the history of human activity in mature forests on less fertile soils deeper in the reserve (McDade & Hartshorn 1984), and in possible consequences for landscape-scale floristic patterns (Clark 1998).

Prior paleoecological studies at La Selva complement and extend archaeological findings. Horn and Sanford (1992, and pers. comm.) found late-Holocene charcoal in both alluvial soils of river terraces and residual soils derived from the andesitic and basaltic lava flows that underlie the reserve (Sollins *et al.* 1994). Additional reports of soil charcoal at La Selva were compiled by Titiz and Sanford (in press), who investigated soil charcoal in an elevational transect between La Selva and the summit of Barva volcano. Within the La Selva reserve, charcoal appears to be most abundant in soils of the more fertile alluvial terraces, where it likely derives from human-set agricultural fires, or possibly cooking fires near habitation sites. Charcoal in the less fertile upland soils of the reserve may reflect human- or lightning-ignited fires that burned intact rain forests during exceptionally dry years (Horn & Sanford 1992). Radiocarbon ages range from 190 ± 40 ^{14}C yr BP to 10,650 ± 50 ^{14}C yr BP (Titiz & Sanford, in press).

Our initial scans of pollen slides prepared from the Cantarrana sediments and those from a second swamp on an alluvial terrace revealed the presence of maize pollen indicating prehistoric agriculture at La Selva (Kennedy & Horn 1997, Horn & Kennedy 2001). Here we report our completed pollen and charcoal analyses of the Cantarrana sediment core. Downcore shifts in the composition and preservation of pollen assemblages, microscopic charcoal concentrations, and the presence of macroscopic charcoal provide a 3200-yr record of human and natural disturbance and likely climate

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variability on an alluvial terrace on the edge of one of the most studied tropical rain forest research sites in the world.

METHODS

STUDY AREA.—Located at the confluence of the Sarapiquí and Puerto Viejo rivers (10°26′ N, 83°59′ W; 35–150 m asl), the 1536-ha La Selva reserve encompasses an area of physiographic and ecotonal transition between the steep foothills of the central volcanic mountain chain and the extensive Caribbean coastal plain (Fig. 1). La Selva falls within the tropical wet forest life zone in the Holdridge classification (Hartshorn 1983a) and contains classic rain forest vegetation: a multilayered, species-rich forest community with abundant lianas, epiphytes, and broad-leaved monocots. Despite the high diversity of trees, La Selva is strongly dominated by a single species, *Pentaclethra macroloba* (Willd.) Kuntze, which occurs with importance values (relative dominance + relative density + relative frequency) of 18–20 percent or higher on a range of site types including swamps, alluvial soils, old alluvial soils, and residual soils (Hartshorn 1983b, Hartshorn & Hammel 1994).

Average daily temperature at La Selva for the period 1983–2004 was 26.0°C (mean minimum 21.4°C, mean maximum 30.6°C). Between 1958 and 2004, annual precipitation ranged from 2892 mm (1995) to 6067 mm (2004), with a mean of 4260 mm (Organization for Tropical Studies, unpublished meteorological data available online at www.ots.duke.edu). Precipitation values are far

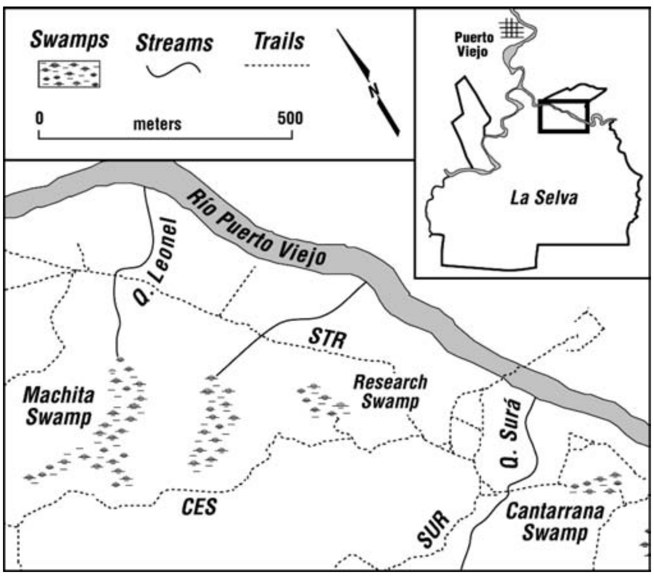

FIGURE 1. Location of the Cantarrana swamp and other swamps on alluvial terraces of the Río Puerto Viejo on the eastern edge of the forest reserve at La Selva biological station, Costa Rica. The reserve is bounded on its eastern and northern edges by fertile alluvial terraces of major streams, as shown on the inset map, but most of the reserve comprises less fertile residual soils away from major streams.

in excess of potential evapotranspiration in all months except February and March, when they are about equal (Herrera 1985). A second short and less-intense dry season (locally called 'veranillo') may occur in September or October, but its regularity and severity are not well documented (Newstrom *et al.* 1994, Sanford *et al.* 1994). Droughts occur sporadically. The most extreme dry event on record occurred between mid-March and early May 1983, when daily rainfall totals were ≤ 5 mm for 48 consecutive days and the April total fell to 16.1 mm, less than 8 percent of the 1958–2004 April mean (Organization for Tropical Studies, unpublished meteorological data). Another marked drought episode occurred in March–April 2000 (30 consecutive days with ≤ 5 mm rainfall). The April 1983 drought occurred during an El Niño year, but not all El Niño years lead to dry conditions in the Caribbean lowlands (Quesada 1992).

La Selva is located within the central Atlantic watershed archaeological area, for which cultural sequences have been described by Snarskis (1981, 1984). The earliest phase, La Montaña (3450–2250 yr BP; see Table 1 for BC/AD equivalents), corresponds to the first securely dated ceramics in the region. La Montaña people were incipient agriculturalists who relied heavily on root and tree crops. Sites associated with the El Bosque phase (2250–1450 yr BP) were larger and vastly more numerous, indicating a population explosion that Snarskis (1984) attributed to a full-scale adoption of maize agriculture and the colonization of new agricultural lands. El Bosque ceramics document increasing social differentiation. The La Selva phase (1450–950 yr BP) is marked by the inception of gold metallurgy, and changes in ceramics and house types that are indicative of further social differentiation. The most recent archaeological phase, La Cabaña (950–400 yr BP), was a time of nucleation of settlements and the emergence of the highly organized caciques or chieftains who ruled Costa Rica at the time of the Spanish conquest.

Local archaeological investigations indicate that prehistoric agriculturalists had settled alluvial terraces at La Selva by at least the La Montaña phase (3450–2250 BP; Sol 2000). Artifacts of all ages at La Selva reserve are almost entirely restricted to the fertile alluvial terraces bordering large streams. Most of the artifacts found at

TABLE 1. *Archaeological phases for the Central Atlantic Watershed archaeological region; after Snarskis (1981, 1984) and M. Sánchez (pers. comm.). Years BP by convention means years before 1950. We follow Sol (2000) in using this chronology for La Selva, although archaeological research elsewhere in the region has called into question the distinctiveness of the El Bosque and La Selva phases, which may overlap in time and involve different social groups rather than a cultural succession (M. Sánchez, pers. comm.).*

	Time span	
Archaeological phase	Years BP	BC/AD
La Cabaña	950–400 BP	AD 1000–AD 1550
La Selva	1450–950 BP	AD 500–AD 1000
El Bosque	2250–1450 BP	300 BC–AD 500
La Montaña	3450–2250 BP	1500 BC–300 BC

La Selva and in the surrounding canton of Sarapiquí are associated with the El Bosque (2250–1450 BP) and La Selva (1450–950 BP) phases. Sol (2000) reported finding a single artifact in the reserve that may date from the earlier part of the subsequent La Cabaña phase. A number of La Cabaña-phase sites have been documented in nearby areas of the Caribbean slope and coastal plain, including the major site of Cubujuquí, located 20 km SE of La Selva (Gutierrez & Mora 1988, Sol 2000), but no other definitive artifacts from this phase are known from La Selva.

CORE SITE AND SAMPLING.—The 0.5-ha Cantarrana swamp (Fig. 1) is located on a lower terrace (~36 m asl, based on La Selva DEM) of the Río Puerto Viejo (Sollins *et al.* 1994). Low perennial herbs dominate the swamp vegetation, with one aroid, *Spathiphyllum friedrichsthalii* Schott, particularly abundant. Scattered shrubs and trees, especially *P. macroloba,* are also present but the persistence of standing water appears to impede woody colonization or survival.

The Cantarrana sediment core was recovered from near the middle of the swamp using a square-rod piston corer (5 cm diameter; Wright *et al.* 1984). One-meter core sections were extruded in the field, and wrapped in a plastic foil and placed in PVC pipes for transport. Core recovery was 80–97 percent in all but the first meter, which upon extrusion was only 48 cm long. We attributed this to compaction and adjusted sampling depths in the upper meter of the core as if compaction had occurred consistently over its length.

LABORATORY ANALYSES.—Core sections were analyzed and archived at 6°C in the Laboratory of Paleoenvironmental Research at the University of Tennessee. We documented core stratigraphy by X-radiography and by visually noting changes in color and texture, and took samples (0.25 cm^3) at ~8-cm intervals for pollen analysis. We processed the samples using standard procedures (HCl, HF, KOH, acetolysis, safranin stain; Berglund 1986), with the addition of *Lycopodium* spores as controls (Stockmarr 1971), and mounted the residues on microscope slides in silicone oil. Duplicate sediment samples were dried at 100°C overnight and ignited for 1 h at 550°C and 1000°C (Dean 1974) to determine water content and estimate organic and carbonate content.

We submitted plant macrofossils from five levels in the core for standard (one sample) and AMS (four samples) radiocarbon dating. Radiocarbon ages were calibrated using version 5.0 of the CALIB program (Stuiver & Reimer 1993) and the data set of Reimer *et al.* (2004). To assign calendar-year (cal yr) ages to specific levels in the core and to zone the pollen diagram using the regional archaeological periodization we used the weighted means of the calibration probability distributions (Telford *et al.* 2004) and linear interpolation.

We counted pollen grains, fern spores, and microscopic charcoal fragments at a magnification of 400× to a minimum sum of 300 pollen grains, exclusive of indeterminates and spores, at 24 levels in the core spaced 8–24 cm apart. Pollen grains were identified to the lowest taxonomic level possible using an extensive regional pollen reference collection created from vouchered herbarium specimens, as well as published keys and photographs of Neotropical pollen types.

Pollen of the Melastomataceae and Combretaceae families were grouped together because of their similar and overlapping morphologies. Within the order Urticales (Moraceae, Urticaceae, Ulmaceae, and Cecropiaceae families) we differentiated *Cecropia, Ficus*, *Trema*, and *Celtis*-type and classified others by pore number. Only oblate, lozenge-shaped grains were tallied as *Ficus* (Horn & Ramirez 1990). Maize pollen was distinguished from other grass pollen based on grain diameter (Horn 2006). Unknown pollen types were assigned a morphotype number; grains were sketched and described and their coordinates on slides were recorded to enable later re-examination. We classified indeterminate pollen grains as corroded, degraded, mechanically damaged, or concealed by detritus (Delcourt & Delcourt 1980). Fern spores were mainly classified by morphology, with a few distinctive types identified to genus. Microscopic charcoal particles were tallied during the pollen counts in two size classes: 5–25 μm and >25 μm in maximum dimension. We attributed only black, completely opaque, and angular fragments to the origin by fire. We checked for the presence of macroscopic charcoal fragments indicative of local fires in each level sampled for pollen by sieving ~10–20 cm^3 of adjacent sediment through nested 250 μm and 500 μm sieves, and examining the retained material under a dissecting microscope. To check for the presence of rare grains of maize pollen, we fully scanned two to five slides from each of the 24 levels in which we carried out full pollen counts, and from an additional 43 levels in the core, using low-power (100×) magnification (Horn 2006). In our low-power scans we also noted the presence of microscopic charcoal.

RESULTS

SEDIMENT STRATIGRAPHY AND CHRONOLOGY.—The Cantarrana sediment core is composed primarily of clay and silt with variable organic content (loss on ignition 8–37%). Wood fragments, charcoal, *Pentaclethra* leaflets, seeds, and other plant macrofossils are abundant in some sections of the core. The base of the core (575–588 cm) is alluvium composed of predominantly sand-sized particles of volcanic rock; our lowest radiocarbon date, on charcoal 12.5 cm above the alluvium, indicates that this material was deposited sometime prior to 3251 cal yr BP (Table 2), when the ancestral Río Puerto Viejo or one of its tributaries flowed through the site now occupied by the Cantarrana swamp. This basal date indicates that the Cantarrana pollen and charcoal record spans the La Montaña, El Bosque, La Selva, and La Cabaña archaeological phases as well as the post-Conquest period (Fig. 2). One of the five radiocarbon dates (β-95552; 1185 cal yr BP) is out of stratigraphic sequence (Table 2). We interpret this to be the result of contamination and reject the date. Sample β-95552 consisted of fragments of *Pentaclethra* leaflets that were sparsely distributed through a 2-cm section of core. We attempted to avoid material near the edges of the core, but some of these leaflets, as a group younger than plant macrofossils in two levels of the overlying 1-m section, may have been carried down from higher in the profile during the coring.

TABLE 2. *Radiocarbon determinations on organic matter from the Cantarrana sediment core. Analyses were performed by the National Ocean Sciences AMS facility (OS numbers) and Beta Analytic Laboratory (β numbers) on uncharred wood (W), charred wood (CW), Pentaclethra leaflets (PL), and charcoal fragments (CF). The date for sample β-54281 is a standard radiocarbon date; others are AMS dates.*

Sample	Depth (cm)	Material	$\delta^{13}C$	Uncalibrated ^{14}C Age (^{14}C yr BP)	Calibrated age (cal yr BP) (2-sigma)	Calibrated age BC/AD (2-sigma)	Relative area under distribution	Weighted mean of probability distribution
OS-4410	222–224	CW	28.47	805 ± 35	779–675	AD 1171–1275	1.0000	721 BP AD 1229
β-54281	412–417.5	W		1570 ± 70	1610–1320	AD 340–630	1.0000	1465 BP AD 485
OS-3546	464–466	PL	29.27	1620 ± 30	1568–1412	AD 382–538	0.9943	1495 BP AD 455
					1592–1588	AD 358–362	0.0057	
β-95592	504–506	PL	30.20	1250 ± 40	1276–1076	AD 674–874	1.0000	1185 BP AD 765
OS-4411	561–562.5	CF	28.21	3030 ± 30	3088–3084	1139–1135 BC	0.0045	3251 BP
					3151–3145	1202–1196 BC	0.0064	1300 BC
					3345–3157	1396–1208 BC	0.9891	

Biopedoturbation by burrowing animals could also explain the presence of this younger material at depth.

POLLEN TAXONOMY AND POLLEN AND CHARCOAL STRATIGRAPHY.—The Cantarrana pollen spectra are taxonomically rich with more than 152 pollen types in 70 families and 120 genera. Many pollen grains were identifiable only to the family level, or to the order in the case of some pollen in the Urticales. Anemophilous taxa are over-represented, compared to their importance at La Selva, as is typical for Neotropical pollen records (Bush 1995), but a large number of

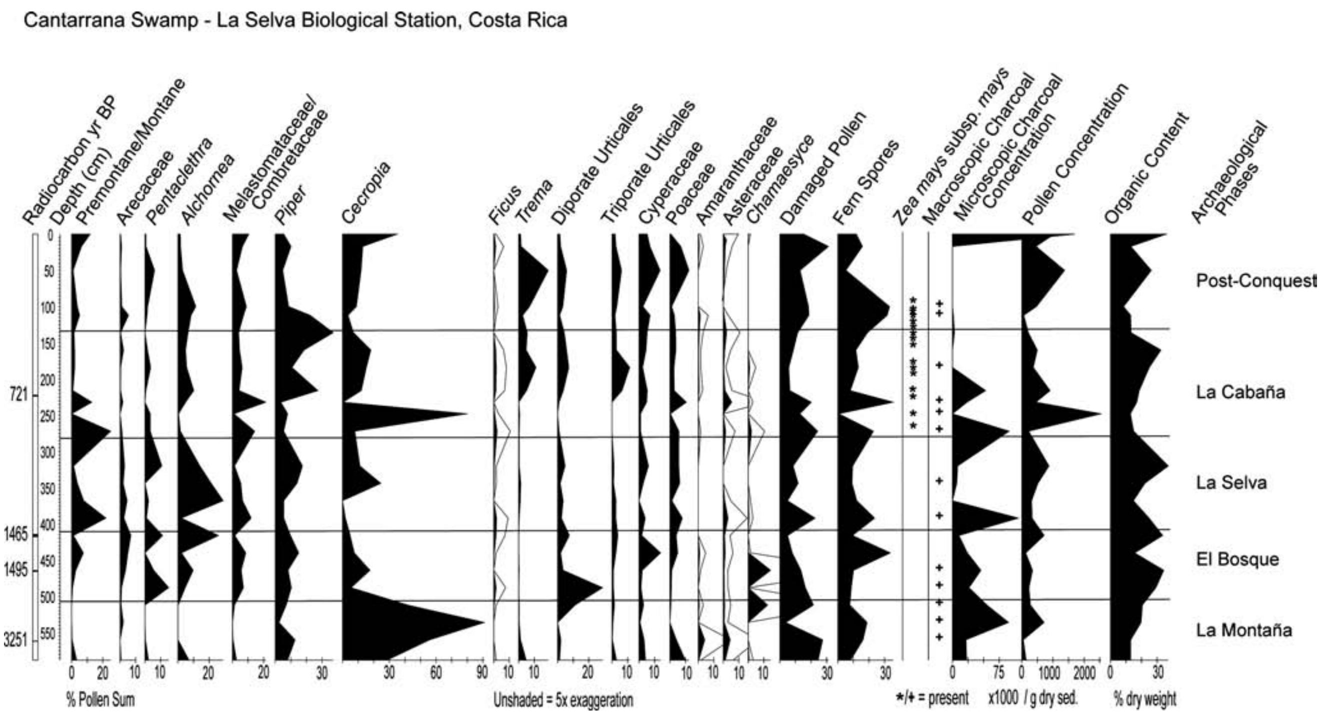

FIGURE 2. Pollen and charcoal diagram for the Cantarrana swamp. Ages are the weighted means of the probability distributions of the calibrated radiocarbon dates (Table 2). The premontane/montane group includes *Alnus, Weinmannia*, *Myrsine*, *Gunnera*, and *Myrica.* Damaged pollen includes indeterminate pollen grains that were corroded, degraded, or mechanically damaged. Pollen percentages are calculated as percent total pollen (excluding indeterminates, except the curve for damaged pollen), while fern spore values are the percent total pollen plus fern spores. Pollen concentrations exclude fern spores and indeterminates. With one exception, the sieved samples that contained charcoal >500 μm also contained charcoal between 250 and 500 μm in size, so we show only the presence of larger fragments here. The concentration of microscopic charcoal in the surface sample was ~175,000 fragments/g dry sediment.

animal-pollinated taxa are also present in the Cantarrana sediments (Kennedy 1998). Most pollen grains derive from lowland wet forest taxa, but two montane genera, *Alnus* and *Weinmannia*, together comprised nearly 5 percent of the total pollen grains counted. In the pollen diagram (Fig. 2) we grouped these with three other genera (*Myrsine*, *Gunnera*, and *Myrica*) that occur primarily at higher elevations (outside the La Selva reserve) as premontane/montane taxa. We also recorded 107 distinctive types of unknown pollen grains that together comprised 1–11 percent of total pollen in the samples. Almost a third were tricolporate reticulate pollen grains, a group that is particularly difficult to identify in the Neotropics (Roubik & Moreno 1991). Pollen concentrations varied throughout the core by two orders of magnitude from 4.98×10^4 to 2.54×10^6 grains/g dry sediment (3.70×10^4–1.36×10^6 grains/cm^3 wet sediment). Pollen preservation also varied substantially. Most indeterminate grains were damaged mechanically, degraded through oxidation, or both. We found 27 grains of maize pollen (*Zea mays* subsp. *mays*, taxonomy as in Sluyter 1997) between depths of 92 cm and 312 cm in our pollen counts and low-magnification scans; grains were 63–87 μm in diameter, with pores 10–14 μm in diameter. These dimensions are within the size ranges of pollen of modern races of Mexican maize and prehistoric maize from other sites in Costa Rica and Mexico, as discussed in more detail by Horn (2006).

We found microscopic charcoal fragments in almost all pollen samples counted or scanned, and macroscopic charcoal fragments in about half of the samples sieved. Surface sediments contained abundant microscopic charcoal but no macroscopic charcoal.

DISCUSSION

PREHISTORIC AGRICULTURE.—The maize pollen in the Cantarrana sediments provides direct botanical evidence of local cultivation of the crop (Horn 2006), likely adjacent to the swamp, beginning ~1070 cal yr BP (~880 AD) in the La Selva archaeological phase, and continuing through the La Cabaña archaeological phases and into the post-Conquest period. The youngest maize grains were found in the lower part of the first core section, where sediments appear to have been strongly compacted. Interpolating from the uppermost radiocarbon date (Table 1) and assuming that sediments compacted uniformly yields an estimated age of ~310 cal yr BP (~1640 AD) for the uppermost maize grains. If the abbreviated length of the first core section is actually due to a gap in recovery rather than compaction, the most recent maize pollen would be only ~110 cal yr BP (~1840 AD). Some combination of compaction and a gap in recovery would date the uppermost maize grains to somewhere between ~110 and ~310 cal yr BP.

Fluctuations in pollen percentages of Amaranthaceae, Asteraceae, Poaceae, and other herbs, and in fern spore percentages, may reflect vegetation disturbance associated with prehistoric agriculture. Peaks for these taxa occur both within and below the Cantarrana 'maize zone,' often in association with peaks in microscopic charcoal and the presence of macroscopic charcoal. Peaks in pollen of *Chamaesyce* (Euphorbiaceae; four species at La Selva, Wilbur *et al.* 1994) may signal opening of the canopy by fire-assisted forest clearance near the swamp; the genus is found almost exclusively in sunny, open places and early-successional sites (Burger & Huft 1995). Agricultural activity, land abandonment, and fire near the Cantarrana swamp would have created patches of disturbed and successional vegetation in which ferns may have been common. Fern spores are noted for long-distance dispersal (Tryon 1970), a characteristic that would be enhanced in a more open, agricultural habitat.

Although the Cantarrana record contains no evidence of maize before ~1070 cal yr BP, the Machita swamp at the head of the Quebrada Leonel (Fig. 1; ~2 km from Cantarrana swamp) contains maize pollen as old as 2600 cal yr BP deposited during the La Montaña and later archaeological phases (Horn & Kennedy 2001). Stable carbon isotope analyses of the Machita sediments revealed shifts in dominant photosynthetic pathways consistent with past forest clearance and maize cultivation (Lane *et al.* 2004). The disturbance indicators in the lower part of the Cantarrana record could derive from agricultural activities at this or another nearby site, or from local cultivation of root crops that left no trace in the sediments.

The fact that few if any La Cabaña-age artifacts have been discovered at La Selva suggests that human population during this last archaeological phase (and subsequent early post-Conquest period) was small. The uppermost maize grains in the Cantarrana core were likely deposited near the end of the period of indigenous occupation at La Selva. The inferred timing of site abandonment suggests that it was a consequence of the Spanish Conquest. Pollen records from other sites in Central America reveal evidence of a reduction or elimination of maize agriculture and of forest regeneration in the last few centuries (Bush & Colinvaux 1994; Clement & Horn 2001; Horn 2007).

FIRE HISTORY.—Charcoal in the Cantarrana sediments may have originated from fires started intentionally by people for agricultural or other uses, or from wildfires ignited by lightning or accidentally by people. The presence of macroscopic charcoal (>500 μm) in about half of the samples analyzed (Fig. 2) indicates that many past fires were local, burning agricultural plots or forests at the margin of the swamp, or possibly even the swamp surface itself under drier conditions. Microscopic charcoal fragments in the Cantarrana sediments (Fig. 2) may represent local or more distant fires. Patterson *et al.* (1987) suggested that most microscopic charcoal in small ponds (<1 ha) derives from the local area, that is, within 20 m or 30 m of the site; however, microscopic charcoal fragments smaller than 50 μm can be transported long distances by wind and may derive from a much larger source area (Clark & Patterson 1997).

The presence of charcoal in most of the Cantarrana samples is consistent with the archaeological and pollen evidence of human activity on alluvial terraces at La Selva and in the broader region throughout the time period represented by the sediment record. Microscopic charcoal is more consistently abundant below the section with maize pollen than within it, and is rare (with one exception) in sediments deposited after ~700 cal yr BP, suggesting higher population levels and greater human activity at La Selva prior to ~700 cal yr BP. Droughts may also have been more intense, longer, or more frequent before 700 cal yr BP, which would have produced conditions more conducive to agricultural burning and wildfires, and perhaps more favorable for the maize cultivation. We interpret the peak in microscopic charcoal in the surface sediment sample to reflect trash burning at the biological station and possibly agricultural and trash burning by station neighbors.

OTHER EVIDENCE OF DISTURBANCE IN THE POLLEN RECORD.—Along with human disturbance, natural disturbances, particularly treefalls, are known to exert significant influence on the structure and dynamics of tropical forests. Canopy trees die standing, are uprooted, snap off and fall, or are fallen upon producing openings in the canopy that allow more light to reach the forest floor and bring about other physical changes in the gap environment. These small-scale disturbances are a source of environmental heterogeneity and may play an important role in the maintenance of species diversity (Denslow & Hartshorn 1994). Hartshorn's (1978) data from long-term research plots at La Selva suggest that gap formation rates may be especially high on alluvial and swamp soils such as those that surround the Cantarrana swamp. Floods, bank collapses, and other riverine disturbances along the nearby Río Puerto Viejo and its tributaries are also likely to increase the frequency of treefalls around the site.

Cecropia (Cecropiaceae) trees are pioneers in treefall gaps and other high-light environments and dominant canopy trees in early-successional sites at La Selva (Hartshorn & Hammel 1994) and in tropical lowlands elsewhere (*e.g.,* Gentry 1993). High percentages of *Cecropia* pollen in sediment records indicate forest disturbance and regeneration processes associated with gap dynamics or with forest clearance and later plot abandonment by prehistoric agriculturalists. *Trema* (Ulmaceae) is also a pioneer species, though not as fast growing (Hartshorn 1983c). Other taxa in the Urticales are more characteristic of mature forests (Burger 1977, Rodgers & Horn 1996). Peaks in diporate and triporate Urticales pollen after ~700 cal yr BP in the Cantarrana record may indicate forest recovery after agricultural clearing.

High pollen percentages of premontane/montane taxa in the central section of the record may reflect opening of the surrounding forest by agricultural clearing, which could have reduced local pollen production and increased the likelihood of long-distance transport of pollen from upslope forests. Studies of modern pollen deposition in lowland Neotropical forests have shown downslope movement of pollen to be relatively rare and typically masked by high production of local taxa (Rodgers & Horn 1996, Bush 2000, Weng *et al.* 2004). However, pollen deposition of taxa from higher elevations might be expected to increase if contributions from local trees such as *Pentaclethra* (below) declined due to forest clearance.

At present, the forest canopy around the Cantarrana swamp is dominated by *P. macroloba*. *Pentaclethra* is pollinated by beetles (Kress & Beach 1994) and has relatively large, sculptured pollen grains. These characteristics suggest that *Pentaclethra* pollen may not be transported far from its source, and that the fluctuating percentages of *Pentaclethra* pollen in the Cantarrana record may indicate shifts in its local abundance. The inverse relationship between the *Pentaclethra* and premontane/montane pollen curves may indicate clearing of local populations by people, which could have reduced the influx of *Pentaclethra* pollen while increasing the influx of premontane/montane pollen from distant forests.

The *Pentaclethra* pollen curve is relevant to a hypothesis about the tree's dominance at La Selva put forward by Janzen (1970). *Pentaclethra* occurs naturally from Nicaragua to the Amazon in three disjunct populations, including one in the Caribbean lowlands of Costa Rica, Panama, and Nicaragua. Janzen speculated that the success of *P. macroloba* at La Selva may be due to its status as a relative newcomer to Costa Rica's Caribbean lowlands. He proposed that the tree may have arrived without its normal complement of seed predators, and that these predators have yet to catch up. Janzen did not give a time frame for the postulated 'recent' arrival of *Pentaclethra*, but from the presence of its pollen in the lowest levels of the Cantarrana core we now know that *Pentaclethra* has been present at La Selva for at least 3200 yr.

Pentaclethra macroloba is presently restricted to relatively infertile soils and swamps within tropical wet and premontane wet forests (0–500 m asl) that lack an effective dry season (Hartshorn 1983b). The continuous presence of *Pentaclethra* at La Selva over the past 3200 yr provides a constraint on the magnitude of past shifts in moisture availability (below). Past droughts could not have been so severe or protracted as to have eliminated mature trees from forests around the Cantarrana swamp.

PAST CLIMATIC VARIABILITY.—Terrestrial and marine sediment records have revealed significant late-Holocene climate variability in the circum-Caribbean region. Oxygen isotope, sediment chemistry, and pollen records from Lake Miragoane, Haiti, and several lakes in the Yucatan Peninsula of Mexico indicate a trend toward drier climate beginning about 3000 yr BP (Hodell *et al.* 2000). Initial isotope records from Yucatan lakes suggested regional dry phases around 2400 ^{14}C yr BP and 1200 ^{14}C yr BP that correlated with evidence of lower lake levels and widespread páramo fires on the Chirripó massif of Costa Rica (Horn 1993, Haberyan & Horn 1999) and with initial dates on soil charcoal from La Selva (Horn & Sanford 1992). The more recent interval has come to be known as the Terminal Classic Drought (TCD) because of its temporal association with the demise of the Mayan civilization. Proxy records of past climate from Yucatan lake sediments and from marine sediments of the Cariaco Basin were originally interpreted to indicate a single, two-century long 'megadrought' of regional scope (Hodell *et al.* 2000, 2005a; Brenner *et al.* 2001). A drought of such duration in the circum-Caribbean would be difficult to reconcile with the continuous presence of *Pentaclethra* and other rain forest taxa in the Cantarrana pollen record. However, new evidence from Lake Chichancanab, Mexico indicates that the TCD consisted of a series of dry events separated by periods of relatively moister climate (Hodell *et al.* 2005a). The shifts in atmospheric circulation that brought dry conditions to the northern Neotropics during the TCD could have affected conditions at La Selva without requiring the wholesale replacement of rain forest by more open woodland or grassland communities that a regional megadrought would seem to demand.

Evidence from Yucatan lake sediments has been interpreted to indicate another period of regional drying in the mid 15th century that is temporally associated with little Ice Age cooling at higher latitudes (Hodell *et al.* 2005b) and that also may have affected climate at La Selva.

Identifying possible signals of climate variability in the Late Holocene pollen and charcoal record from the Cantarrana swamp is complicated by the strong overprint of human activity, which can mask or mimic evidence of climate change (Horn 2007). Based on the chronology from the Chichancanab record, the TCD overlapped the latter half of the La Selva archaeological phase and the early part of the La Cabana archaeological phase, with the main dry phases (each themselves comprised of wet and dry intervals) occurring from 1180 to 1080 cal yr BP and 1030 to 850 cal yr BP (Hodell *et al.* 2005a). The greater importance of both microscopic and macroscopic charcoal in the Cantarrana record prior to ~700 cal yr BP and the scarcity of macroscopic charcoal younger than this in soils anywhere at La Selva (Titiz & Sanford, in press) is consistent with the idea of regionally drier climate during the TCD and at intervals prior to this time (but the charcoal evidence does not support evidence of drying during the 15th century).

Peaks in the pollen of the herb *Chamaesyce* and increased percentages of weedy herbaceous taxa in the Asteraceae family prior to 700 cal yr BP could indicate hydrological shifts, in addition to agricultural activity in adjacent forests. Lowering of the water table in the swamp would allow herbaceous colonization of the swamp surface. In the seasonally dry lowlands of northwestern Costa Rica, one species of *Chamaesyce* is known to colonize the surface of the Palo Verde marsh during the dry season (Hernández & Gómez 1993).

The strongest evidence of past droughts in the Cantarrana record may be the marked downcore shifts in pollen preservation, pollen concentration, and organic content. Under certain environmental conditions, chemical and biochemical oxidation can degrade, corrode, and weaken the exine (outer layer) of pollen grains, making them more susceptible to breakage or crumpling (mechanical damage) by sediment compaction (Cushing 1963). Delcourt and Delcourt (1980) found that high percentages of degraded and mechanically damaged pollen grains, along with low organic content, in sediment profiles from the southeastern USA coincided with relatively dry periods. In the Cantarrana record, peaks in damaged pollen grains in levels with low organic content and low intact pollen concentrations indicate hydrological shifts that created conditions unfavorable for pollen preservation. The timing of droughts that would produce such shifts is less clear because deep drying can affect pollen preservation below the surface of a swamp in samples that represent earlier time periods. The downcore variability in these indicators suggests the occurrence of multiple past dry periods.

At present, water stands in the Cantarrana swamp most of year, although the water table sometimes drops below the surface during the short dry season. Both organic content and pollen concentration are relatively high in the surface sample representing modern conditions; lower values may reflect longer or more extreme dry seasons during which the water table was lowered far enough or long enough to permit oxidation and other damage to pollen grains. Synchronous peaks in damaged pollen and in fern spores in some levels support this interpretation. Fern spores are more resistant to oxidation than pollen grains (Dimbleby 1985) and are likely to reach higher percentages in sediments deposited at times of lower water levels, although increases may also be linked to forest clearance and fires. In this context, it is interesting to note the strong peak in fern spores just prior to uppermost occurrence of maize pollen and macroscopic charcoal. This peak is coincident with increased percentages of damaged pollen, low pollen concentrations and organic content, and a striking decrease in *Piper* pollen. Interpolation between the present day surface and our uppermost date would put these shifts at ~350 cal yr BP, which allows for the possibility that they reflect the 15th century (~500 cal yr BP) dry period discussed by Hodell *et al.* (2005b).

Conclusion.—The Cantarrana pollen, spore, and charcoal profiles, and other characteristics of the sediment record, support the current conception of tropical rain forest as a highly dynamic ecosystem influenced by both human and natural disturbances. Our results contribute to efforts to understand the long-term history of tropical research areas and the possible ecological legacies of prehistoric and historic human land-use patterns. The alluvial terrace surrounding the Cantarrana swamp at the La Selva biological station is designated as an ecological reserve and has been regarded as especially pristine (McDade & Hartshorn 1994), but our results indicate with certainty that at least part of this area was cleared and cultivated by prehistoric agriculturalists. The pollen evidence of maize cultivation at the Cantarrana swamp extends the local archaeological record by documenting prehistoric human occupation of La Selva during the La Cabaña archaeological phase. Additional paleoecological and paleoclimatic information from La Selva is needed to place our findings of human activity on the edge of the reserve into context. How prehistoric peoples who farmed alluvial terraces at La Selva used forest on residual soils away from major rivers, and how this 'human footprint' would be evidenced in the modern forest composition (Clark 1988), remain intriguing questions for future biological and paleoecological research.

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