# Forests, fields, and the edge of sustainability at the ancient Maya city of Tikal

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Tikal has long been viewed as one of the leading polities of the ancient Maya realm, yet how the city was able to maintain its substantial population in the midst of a tropical forest environment has been a topic of unresolved debate among researchers for decades. We present ecological, paleoethnobotanical, hydraulic, remote sensing, edaphic, and isotopic evidence that reveals how the Late Classic Maya at Tikal practiced intensive forms of agriculture (including irrigation, terrace construction, arboriculture, household gardens, and short fallow swidden) coupled with carefully controlled agroforestry and a complex system of water retention and redistribution. Empirical evidence is presented to demonstrate that this assiduously managed anthropogenic ecosystem of the Classic period Maya was a landscape optimized in a way that provided sustenance to a relatively large population in a preindustrial, low-density urban community. This landscape productivity optimization, however, came with a heavy cost of reduced environmental resiliency and a complete reliance on consistent annual rainfall. Recent speleothem data collected from regional caves showed that persistent episodes of unusually low rainfall were prevalent in the mid-9th century A.D., a time period that coincides strikingly with the abandonment of Tikal and the erection of its last dated monument in A.D. 869. The intensified resource management strategy used at Tikal-already operating at the landscape's carrying capacity-ceased to provide adequate food, fuel, and drinking water for the Late Classic populace in the face of extended periods of drought. As a result, social disorder and abandonment ensued.

paleoecology | Neotropics | paleoethnobotany | irrigation | root crops

The Late Classic period (A.D. 600–850) was a time of unprecedented architectural, astronomical, and artistic achievement at Tikal, one of the leading urban centers of the ancient Maya realm. It was also a time of meteoric population growth at this bustling cultural center. Notwithstanding its prominence as a major Maya polity, how Tikal's leaders and farmers managed to provide food, fuel, and other sustenance for its many occupants has never been fully understood or quantified.

To best assess resource potential at Tikal, we first defined an extraction zone that was extrapolated from archaeological settlement data by creating a Voronoi diagram (1, 2) (Fig. 1). Essentially, this approach proscribes a proportional boundary between Tikal and its surrounding contemporaneous communities: namely, Motul de San Jose, El Zotz, Uaxactún, Xultun, Dos Aguadas, Nakum, Yaxha, and Ixlu. Using this technique, including assigning greater economic clout to Tikal using a 2:1 weighting scheme (see section on the Voronoi diagram in *SI Materials and Methods*), we calculated that its Late Classic resource extraction zone encompassed ~1,100 km<sup>2</sup>. This is the area from which the residents of Tikal could obtain their necessary food, fuel, construction timbers, and other living essentials.

Superimposing the Voronoi Diagram over satellite images of modern Tikal (2, 3) (Fig. 1), which is mostly forested today, reveals that  $\sim 850 \text{ km}^2$  is upland tropical forest habitat and 250  $km^2$  is seasonal wetland or bajo (4).<sup>†</sup> Pollen data from Lake Petén Itza (5), a deep lake that is downwind and less than 5 km south of the extractive zone of Tikal, suggest that the range of forest clearance was from 60-70% during the Late Classic period (LCP). As with all calculations in this report, we used the most conservative number when a range of values is available. In this case, we use the 60% figure for the amount of upland forest cleared during the LCP, leaving ~340 km<sup>2</sup> of forest intact. Pollen data from Aguada Vaca de Monte (Fig. S1), a small pond located in the Bajo Santa Fe with a pollen content more reflective of the surrounding bajo, suggested that 37-32% of the bajo lands (80 km<sup>2</sup> using the figure of 32%) were cleared for agriculture and another 170 km<sup>2</sup> remained as managed seasonal swamp forest (Fig. S2). Details of the pollen analyses are given in the section on palynological data in SI Materials and Methods.

## Significance

The rise of complex societies and sustainable land use associated with urban centers has been a major focus for anthropologists, geographers, and ecologists. Here we present a quantitative assessment of the agricultural, agroforestry, and water management strategies of the inhabitants of the prominent ancient Maya city of Tikal, and how their land use practices effectively sustained a low-density urban population for many centuries. Our findings also reveal, however, that the productive landscape surrounding Tikal, managed to the brink of its carrying capacity during the Late Classic period, did not have the resilience to withstand the droughts of the 9th century. These results offer essential insights that address the question of why some cities thrive while others decline.

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<sup>1</sup>We are fully aware that the forest structure of the northern Petén is more complex than this simple dichotomy. Other studies of the area have subdivided the forest differently, for example Ford's survey of the Tikal-Yaxha transect divided the landscape into three classes (4). For our purposes of calculating standing biomass, we surveyed the forests extensively and bifurcated the forest cover into two classes (upland and bajo) that could be readily discerned on Landsat Enhanced Thematic Mapper Plus (ETM+) imagery.



Fig. 1. Tikal extraction zones. The Voronoi cell equal to the extractive zone during the LCP is outlined in cyan and in yellow for the Late Preclassic period. The built environment of the city, the portion that contained the majority of houses, temples, ball courts, and other structures during the LCP (in red) was determined by archaeological survey (3). The black square outlines the 9 km<sup>2</sup> of the ceremonial core mapped by Carr and Hazard (2). Note that of the eight neighboring Maya polities used to create the LCP Voronoi diagram, Xultun is not listed. It is outside the borders of this map to the northeast of the Voronoi diagram.

## Agroforestry

Because forests supplied essential resources, such as fuel (Table S1), construction material, habitat for game, wild plant foods, and a pharmacopoeia from medicinal species, the study of past methods of agroforestry is crucial to understanding the economic underpinning of the ancient Maya. As part of this study, above ground biomass (AGB) survey transects of modern forests were combined with Landsat 7 multispectral imagery and statistically modeled to yield biomass estimates for the Tikal region. The AGB of modern upland forest was calculated at  $28.9 \pm 2.6$ million kg·km<sup>-2</sup> (SEM) and 18.2  $\pm$  0.523 million kg·km<sup>-2</sup> (SEM) for bajo forest. If we use these data to estimate the AGB of the LCP Tikal forest, with forest extent determined by pollen data, we find that 9.8 billion kg of wood would have been present in the uplands (on 340 km<sup>2</sup> of forested land) and 3.2 billion kg in the bajos (on 170 km<sup>2</sup>) during the LCP. It is reasonable to use the modern Tikal forest as an analog for the ancient forest because the archaeological wood assemblage (Table S2) showed a remarkable similarity to the oligarchic species of the modern forest (Table S3). See the sections on modern forest surveys, biomass calculations, and ancient wood use in SI Materials and Methods for expanded discussions.

If the ancient forests were managed on a sustainable basis, and there is ancient tree-ring evidence that the Maya attempted to do so (6), then the Tikal occupants could only have harvested the annual growth increment each year. To calculate the annual growth rate of Tikal forests, we extrapolated from the results of a 10-y study (7) of a 50-ha plot in a similar type of Central American moist tropical forest on Barro Colorado Island, Panama (BCI), where it was recorded that the biomass change rate was 0.55 Mg·ha<sup>-1</sup>·yr<sup>-1</sup>. Because the modern Tikal forest had a larger basal area (39 m<sup>2</sup>·ha<sup>-1</sup>) than the BCI forest (28 m<sup>2</sup>·ha<sup>-1</sup>), a proportional adjustment to 0.76 Mg·ha<sup>-1</sup>·yr<sup>-1</sup> was performed. Using these forest growth data, we calculated that the amount of sustainably usable wood on an annual basis during the LCP would have averaged 26 million kg·yr<sup>-1</sup> in the uplands and 13 million kg·yr<sup>-1</sup> in the bajos for a total of 39 million kg·yr<sup>-1</sup> (8) (Table 1). Justification for using forest growth data from BCI can be found in the section on annual growth increment calculations in SI Materials and Methods.

By far the heaviest demand on the forest was firewood needed for cooking. All of the major foods of the ancient Maya, especially beans, root crops, and to a lesser degree, maize had to be cooked before consumption. This requirement created a daily and inexorable fuel need for all of the Tikal inhabitants. The firing of ceramics also required substantial amounts of fuel. Studies at well-preserved Maya archaeological sites (9, 10) revealed that each household, from the most humble to the elite, possessed from 70 to 80 ceramic vessels at any given time. In addition, the use life of a ceramic pot was only about 1 y on average (11, 12). To make matters worse, the kilns used by the Tikal Maya were inefficient (13), even by preindustrial standards, and required about 5.2 kg of fuelwood per vessel (14). Thus, keeping the city supplied with pottery, not to mention the possibility of export production, created a heavy demand for fuel. The production of lime (calcium oxide), an essential component of plaster, also required considerable fuel input; it was made by burning crushed limestone and required 5 kg of wood to make 1 kg of lime (15). All of the temples, plazas, causeways (sacbeob), reservoirs, and elite houses were covered with plaster and, although this was not a daily need, in the long run the process consumed a substantial amount of fuel. Wood required for construction timbers and artifact manufacture created an essential, but less voluminous demand. Details of these calculations are provided in the section on ancient wood use in SI Materials and Methods and the results are summarized in Table 1 and Table S1.

The estimated wood quantities required annually for the maintenance of LCP populations at Tikal for fuel and construction was 42 million kg·yr<sup>-1</sup>, approximately equal to the amount of wood available on a sustainable basis (39 million kg·yr<sup>-1</sup>) from the Tikal upland and bajo forests. The Maya could have compensated for any shortages in forest productivity through the importation of pine wood (see section on ancient wood use in *SI Materials and Methods*) and intensive forestry techniques applied to a fixedplot agroforestry system. [Evidence from burned wood retrieved

Aboveground biomass	Uplands	Bajos
Modern AGB	$28.9 \pm 2.60 \times 10^{6} \text{ kg} \cdot \text{km}^{-2}$	18.2 ± 0.523 million kg·km <sup>-2</sup>
LCP Tikal total area	850 km <sup>2</sup>	250 km <sup>2</sup>
Forest cover (LCP)	340 km <sup>2</sup>	170 km²
Forest AGB (LCP)	$9.8 \times 10^9$ kg	$3.2 \times 10^9$ kg
Sustainably usable AGB (LCP)	26 × 10 <sup>6</sup> kg⋅yr <sup>-1</sup>	13 × 10 <sup>6</sup> kg yr <sup>−1</sup>
Total annual usable AGB (LCP)	39 × 10 <sup>6</sup> kg·yr <sup>-1</sup>	
Total annual wood need (LCP)	$42 \times 10^6 \text{ kg} \text{ yr}^{-1}$	

Results are based on modern vegetation surveys coupled with pollen data to determine the forest extent during the LCP. Wood use requirements for LCP Tikal are based on the estimate of 45,000 occupants (8).

from middens and structures at Tikal indicate that forests were being managed as fixed plots or woodlots. Most (90%) of the archaeological charcoal samples examined (n = 421) had parallel rays when viewed in transverse section, indicating that they were from mature trees, not saplings or branches, which have convergent rays, a condition that would be expected in young second growth forest. Only 3% of archaeological wood samples had rays that were clearly convergent (the other 7% were classified as indeterminate). Accordingly, the Tikal Maya appear to have been harvesting mature trees for fuel and construction purposes.]

Table 1. Wood availability

# Agriculture

The ancient Maya agricultural practices at Tikal can be interpreted with fresh and previously unavailable insights by using the extraordinarily well-preserved Late Classic village of Cerén (9) as a comparative model. Although Tikal operated on a much larger scale, the comparison is valid because both communities used essentially the same array of crops (Table S2), and they occupied land with similar native vegetation and elevation. As at Cerén, the built environment of Tikal (160 km<sup>2</sup>) would have been cleared of its native forest cover and planted with dooryard gardens. Crops used at Tikal included maize (Zea mays L.), three species of beans (Phaseolus spp.), two species of squash (Cucurbita spp.), and several species of root crops, including sweet potato (Ipomoea batatas [L.] Lam.) (16) (Fig. 2), achira (Canna cf. indica L.) (Fig. S3), and malanga (Xanthosoma sagittifolium [L.] Schott.). Manioc has not been identified at Tikal, but this important root crop has been discovered at other nearby sites (17, 18), so it seems quite likely that the farmers of Tikal had access to it as well. Paleoethnobotanical remains of fruit trees from Tikal also parallel the Cerén model, with orchards of coyol (Acrocomia aculeata Lodd. ex. Mart), sapote (Pouteria sapota [Jacq.] H. E. Moore & Stearn), jocote (Spondias cf purpurea L.), nance (Byrsonima crassifolia [L.] H.B.K.), avocado (Persea americana Mill.), and curiously, cacao (Theobroma cacao L.) (19). [Cacao was an important product to the ancient Maya and the iconographic references to it at Tikal and elsewhere are numerous. Yet it is believed (19) that cacao, which is intolerant of long periods of dryness, could not have survived the long, hot dry season at Tikal. Evidently, this supposition was untrue because among the archaeological sediments at Tikal, we not only found the seeds of cacao (which easily could have been imported), but we also recovered the burned wood of cacao (Fig. S4), which would not have been imported. Two of the shade trees that are often grown with cacao, Gliricidia sepium (Jacq.) Steud., and Erythrina spp. were also found among the archaeological plant remains at Tikal. These trees are leguminous symbionts, traditionally associated with cacao production, which not only provide cover for the shade-loving cacao, but bear nitrogenfixing bacteria in their root nodules that help to fertilize the soil as well. Cacao and its symbionts were probably grown in special areas, such as artificial sinkholes or rejolladas, where they were protected from the heat and could be watered during the dry season.] As at Cerén, these orchards would have been planted adjacent to household compounds that were widely spaced at Tikal.

Relying on Cerén as an interpretive model, intensively managed fields of maize, other seed crops, and root crops (Table S2) that provided most of the calories for the city were found outside of the built environment of Tikal (the zone in red in Fig. 1). Previous studies (20) of Petén farmers recorded that an average of 0.18 ha was required to feed an individual using traditional farming techniques. If we apply this figure to the LCP Maya, then Tikal required  $\sim 80 \text{ km}^2$  of fertile land per year to feed itself  $(0.0018 \text{ km}^2 \times 45,000 \text{ inhabitants})$  (8). Looking at the upland areas only, and assuming an intensive, open field style of agriculture, the Tikal Maya would have had enough land for 1 y of planting with about 270 km<sup>2</sup> of vacant, cleared land in any given year, enough for about 3 y of fallow. A short fallow system as described by Sanders (21) in a 1:3 ratio of planting to fallow years or a ratio of 3:5 as described by Griffin (22) would have been feasible within the confines of available upland planting surfaces. Killion's (23) observations of intensive, fixed-plot agriculture with short fallow periods in southern Veracruz seem to closely match the projected conditions at LCP Tikal.

Some scholars (24) have stated that this kind of short fallow system would not have been sustainable. Others (25), however, have observed that alternative long fallow systems would not have been possible in the Late Classic Maya Lowlands; there just was not enough land. Short fallow systems could have been used



Fig. 2. Electron micrograph of a burned sweet potato (*lpomoea batatas*). Characteristically in sweet potato roots, the tissue organization is disrupted by the formation of radially oriented cavities (as seen in this image) when carbonized (16). This sample from Middle Preclassic Tikal represents the first evidence for sweet potato in the ancient Maya Lowlands. It was accelerator mass spectrometry radiocarbon dated to cal 640  $\pm$  30 B.C. (SD).



Fig. 3.  $\delta^{13}$ C isotope enrichment. Map showing the location of the Perdido Reservoir and its relationship to the pocket bajo to the south/southwest. Sedimentary evidence in the Pocket Bajo (Fig. S5) and unusually high amounts of debris in the Perdido Reservoir indicate that the tank was used for irrigation. Episodes of  $\delta^{13}$ C enrichment in the pocket bajo are compatible with the interpretation of maize agriculture. The base map is from Carr and Hazard (2), courtesy of the University of Pennsylvania Museum of Archaeology and Anthropology.

if managed carefully with yields declining slowly over time (26). To facilitate production in a short fallow system, Tikal farmers cultivated at least three species of leguminous annual crops (Table S2). A common practice among modern Maya farmers is to plant fields with multiple crops, including nitrogen-fixing cultigens and maize. Tikal farmers, because they had all a full array of nitrogen-fixing crops, likely used this same technique. These leguminous plants provide accessible nitrogen in soil and help prevent yield declines common in short fallow agricultural regimes.

Phosphorus, however, is a critical element often in short supply across the Maya Lowlands (27). When forest cover is removed, the topsoil is gradually starved of this essential nutrient (28), an outcome with potentially catastrophic consequences for ancient Maya farmers (29, 30). Fortunately for the people of Tikal, soils may have been naturally renewed via the capture of windblown soot, dust, and volcanic ash. Analyses by X-ray diffraction and X-ray florescence of reservoir sediments from Tikal demonstrate that there were sporadic but substantial inputs of aeolian volcanogenic materials deposited throughout the Classic period (31). This regular deposition of volcanic ash may well have served to ameleorate exausted agricultural soils at Tikal and helps to explain how intensive farming practices could have succeeded for extended periods of time without rapidly declining yields.

To be sure, the uplands were not the only areas cultivated; there were also agricultural activities in the seasonal wetlands. Pollen data from Aguada de Terminos (Fig. S3) reveal that maize and achira (*Canna* cf. *indica* L.) were grown in that sector of Bajo Santa Fe, demonstrating that portions of the bajos, especially the margins, were active areas of intensive agriculture. Chert-lined terraces, created to prepare planting beds and prevent soil from eroding down the hillslope, were found near the adjacent Terminos plazuela group (Fig. S6) and signify a high level of labor investment in bajo agriculture. In an area with a pronounced annual dry season and no permanent rivers or lakes in the immediate vicinity, water was a scarce and highly valued resource. Tikal grew as a city around a system of springs emanating from what is now the Temple Reservoir, which sits at the head of a long ravine (32). Through time the ravine was blocked off in places with the purpose of impounding water that flowed from the springs. As Tikal continued to grow, they built large plazas on either side of the ravine and canted the pitch of the pavements so that seasonal rainwater would flow into the reservoirs.

This elaborate system designed for water retention gave rise to another form of intensive agriculture south of the Perdido Reservoir (Fig. 3), where impounded water appears to have been used to periodically flood a pocket of flat land located just below the tank and its egress. One of the smallest of the formal tanks identified, Perdido, evidently functioned exclusively as a source of agricultural irrigation water, as inferred by the debris recovered from our excavations. Compared with other Tikal reservoirs, several times the amount of artifactual waste was found having washed into the Perdido tank. This was not a reservoir that was kept clean for potable water as seen elsewhere at the site.

An ancient agricultural field locus 100–900 m south/southwest of the Perdido Reservoir was identified lying stratigraphically lower than the bottom of the plaster floor of the reservoir and the bottom of the egress gate. Both the plaster floor of the reservoir and the stratified base of the agricultural field date to sometime between A.D. 350 and 550. The soil profile (Fig. S5) from the former agricultural field was especially telling. Bajo-like soils were abruptly truncated around A.D. 485 (just prior to the beginning of the LCP) and then were overlain by stratified alluvial sediments. We interpret these laminated alluvial strata as evidence for repeated bouts of flooding from the reservoir, ostensibly for agricultural purposes.

Furthermore,  $\delta^{13}$ C values associated with Classic period land surfaces and rooting zones in three soil pedons located between 500 and 800 m south of the reservoir show clear signs of enrichment (Fig. 3). Soil samples for isotopic analysis were collected from Pedon 1 in the Pocket Bajo to a depth of 90 cm and results revealed two peak shifts in  $\delta^{13}$ C values compared with the surface reading: one of 4.3‰ at a depth of 30 cm and 4.7‰ at a depth of 75 cm. This pattern in the C isotope data suggest two separate periods of C<sub>4</sub>-dominated plant cover. Results from Pedon 2, only 45-cm deep, reveal a  $\delta^{13}$ C shift of 2.7‰, which is inconclusive for the presence or absence of C<sub>4</sub> plants. Pedon 3, however, which is located just to the east of Pedon 2, revealed strong isotopic evidence of ancient C<sub>4</sub> plants with a  $\delta^{13}C$  enrichment as high as 6.1‰. Pedon 4 was close to house structures and the upward shift of 3.3% in  $\delta^{13}$ C provided some evidence of ancient  $C_4$  plants. Details of the radioisotopic methodology are presented in the section on stable carbon isotope in SI Materials and Methods.

These data, considered together, indicated that C<sub>4</sub> plants were growing for long periods within the Perdido Pocket Bajo. Because our surveys of the modern vegetation in the pocket bajo recorded no C<sub>4</sub> or Crassulacean acid metabolism (CAM) plants, our analyses of archaeological plant remains revealed no C<sub>4</sub> cultigens (other than maize), and the  $\delta^{13}$ C results showed evidence of  $C_4$  enrichment, our interpretation of these multiple strands of evidence is that the Pocket Bajo was an ancient agricultural field and maize likely was one of those plants cultivated. (In addition to maize, there are other C<sub>4</sub> and CAM plants in the Neotropics that could have caused the  $\delta^{13}C$  enrichment. It is possible that the land was cleared in the past and some weedy C<sub>4</sub> plants, such as wild amaranth, sedges, or wild grasses, invaded the field and caused the  $\delta^{13}$ C enrichment. In either case, whether it was maize or some other crop intermingled with weedy C<sub>4</sub> plants, all of the evidence considered together indicate that the land below Perdido Reservoir was periodically flooded for agricultural purposes during the Classic period.) Using water released from the Perdido Reservoir during the dry season, the Tikal Maya could have double-cropped the area and obtained a second harvest from this carefully tended pocket of land.

Land below the Corriental Reservoir also appears to have been a likely location for crop irrigation. A switching station, probably used to divert water downstream to arable land surfaces, was found at the low end of the reservoir (32). Other locations where irrigation was feasable included areas below the Bejucal and Tikal reservoirs, which lie just slightly higher in elevation than broad flat areas of deep soil. There may have been other reservoirs at Tikal that were used for irrigation but these four, at least, were well situated for it.

### Discussion

One of the conclusions that can be drawn from the evidence generated is that the Maya at Tikal were living quite near or perhaps beyond the sustainable carrying capacity of their highly engineered landscape. Larger population estimates (33–35) than the one used in our calculations for LCP Tikal would not have been feasible without massive importation of food and fuel from outside the defined extraction zone. This importation seems highly unlikely, given the absence of navigable waterways, draft animals, or wheeled vehicles (36). Although there is abundant evidence for the long-distance movement of highly valued trade goods, such as salt (37, 38) and cacao (39), the movement of lowvalue bulk goods probably was very localized (40).

The reservoir system had the positive effect of maximizing and carefully storing the rainwater that fell on the site core, but had the negative effect of cutting off recharge supplies to the springs, once a major attraction to early settlers. During most of the 7th and 8<sup>th</sup> centuries, precipitation was abundant enough to accommodate crops as well as reservoir recharge to provide for the needs of a growing populace. Although these adaptations were extremely effective in meeting the short-term demands of population growth and increasing levels of social well-being, the unforeseen consequences of the extensive landscape alterations had tragic results.

By the early to mid-9th century (A.D. 820-870), speleothem evidence indicates that an extremely dry period akin to episodic drought (41-43) occurred in the central Maya Lowlands. This multidecadal drought coincides with the depopulation of Tikal (43). The last dated monument was erected in A.D. 869 (44), when the city was already in its death throes (45). Moreover, the drought was likely anthropogenically influenced, as there is a growing body of evidence that indicates forest clearance, even partial forest clearance, will negatively impact the hydrologic cycle (46-48). In short, the construction of extensive pavements combined with forest clearance likely exacerbated the effect of the drying trend, so by the mid-9th century there were inadequate supplies of water and food with little resilience left in the system to adapt to new conditions. As a consequence, the social structure of Tikal collapsed, leaving the site core abandoned with only a tiny relict population huddled around the few water holes that did not dry up. Although the focus of our study has been the polity of Tikal, what we describe was not an isolated event; similar scenarios of human interaction with the environment and climate change played out on a broader scale throughout much of the Central Maya Lowlands at the end of the Classic period (30, 49).

Although some may view this interpretation as environmental determinism, we argue that the demise of LCP Tikal was a product of human agency where a carefully constructed niche was designed to meet the immediate needs of a burgeoning population. Ultimately, through the long arc of time as climatic patterns changed, with influences from human activities, the intensified agricultural, hydraulic, and agroforestry systems that made the urban condition possible at Tikal reached a tipping

point and were unable to meet productivity demands in the face of reduced precipitation.

### **Materials and Methods**

During our 2009 and 2010 field seasons, we surveyed modern forests at Tikal to determine the number, size, and diversity of tree species. Forest surveys were conducted, mostly in 500-m<sup>2</sup> rectangular plots, and covered a total of 5.95 ha in a variety of forest types. The diameter at breast height, tree height (assessed with a hand-held clinometer), and species name for each tree over 6 cm diameter at breast height were recorded within each plot demarcated with a GPS unit. Voucher specimens were collected for tree species and brought to the paleoethnobotanical laboratory at the University of Cincinnati for further identification. Vouchers were compared with herbarium specimens at the Margaret H. Fulford Herbarium at the University of Cincinnati (CINC) and the Missouri Botanical Garden Herbarium. For specimens that were difficult to identify, nuclear and chloroplast DNA was extracted from voucher leaves and sequenced for final identification (48). Sequences were compared with the Basic Alignment Search Tool (BLAST) from the National Center for Biotechnology Information database. Vouchers were housed at the University of San Carlos Herbarium and CINC as part of their permanent collections. Biomass of forest tracts was determined using satellite images in combination with

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ground surveys. Environmental indices and data transforms were derived from the spectral data of a March 2003 Landsat 7 ETM+ image of the study area obtained from the US Geological Survey Global Visualization Viewer (GLOVIS; glovis.usgs.gov). Excavations and coring procedures focused on the recovery of paleoethnobotanical remains and the collection of archaeological sediments through time. Archaeological wood and other plant remains were examined with a combination of light and environmental scanning electron microscopes (Philips XL30 ESEM). Soil samples were analyzed for pollen content, isotopic signatures ( $\delta^{13}$ C and  $^{14}$ C), and chemical composition using powder- X-ray diffraction and X-ray florescence. Additional details of our research methods can be found in the *SI Materials and Methods*.

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