# **Supporting Information**

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### **SI Materials and Methods**

**Voronoi Diagram.** Determining the territory controlled by an ancient polity is a difficult problem for which only imperfect solutions can be offered (1). Hieroglyphic inscriptions can sometimes offer information about interpolity relationships, including glimpses of political hierarchies, warfare, and royal marriages (e.g., ref. 2), but such texts, even where preserved, seldom contain information relevant to the ancient functional economy, nor the nature or extent of a polity's effective resource extraction area. Thus, we are left to reconstruct ancient economic zones using archaeological proxies.

One approach to modeling ancient political and economic spheres is through spatial analysis of archaeological settlement data. This approach provides one way to model ancient political and economic spheres. For example, the relative size of ancient communities at various points in time offers information about the labor and resources they controlled. Given the general similarity in residential density at most Maya sites, the areal extent of settlement can be used as a rough proxy for population size. Similarly, the volume of monumental architecture constructed at a site during a given time period can be used as a proxy for the amount of labor and resources controlled by the site's rulers.

For ancient Tikal, we attempted to reconstruct the size of its territory or primary economic extraction zone for two points in time: about A.D. 100, the apogee of the Late Preclassic period, and about A.D. 700, the peak of Tikal's regional influence in the Late Classic period (LCP). In both cases, we used available archaeological and epigraphic data to determine Tikal's nearest neighbors that were large enough to exert an appreciable degree of economic autonomy. Because evidence indicates that none of these neighboring sites was either as large or regionally dominant as Tikal during the two times considered, we posited that their own zones of economic control did not extend as far as that of Tikal, or some of their economic production went toward supplying the needs of Tikal. Hence, for modeling purposes we weighted the extent of territories in favor of Tikal two-thirds to one-third.

The amount of archaeological and epigraphic information available for Tikal's neighbors varies tremendously. Data have been available for many years for Uaxactun (3, 4), and Yaxha (5, 6). Excavation data are now forthcoming for El Zotz and El Palmar, Nakum (7), and Xultun (8). However, for most neighboring sites data are more preliminary, derived chiefly from early expeditions (9, 10), the University of Pennsylvania Tikal Project peripheral surveys (11–14), Instituto de Antropología e Historia de Guatemala site inventories (15, 16), and surveys of the Rio Holmul drainage and intersite transects between Tikal, Yaxha, and Nakum (17–20). The Tikal Project surveys and those of Ford (17) and Fialko (19, 20) included a few test pit excavations to obtain chronological data, but the other projects examined only surface features, inscribed monuments, and sometimes looter's trenches.

For the Late Preclassic zenith (ca. A.D. 100), Tikal's nearest competitive neighbors appear to have been Zocotzal, El Palmar, El Encanto, Jimbal, and Chalpate (also known as Ramonal). At the time, each of these centers included between two and four architectural attributes associated with major centers: triadic groups, pyramid complexes, ball courts, and intrasite *sacbeob* (causeways). For the Late Classic apogee (ca. A.D. 700), most of these Preclassic sites were either abandoned or subsumed as suburban or satellite centers of Tikal as it expanded its political and economic power. In this later period, Tikal's likely nearest

competitive neighbors lay at greater distances: Motul de San Jose, El Zotz, Uaxactun, Xultun, Dos Aguadas, Nakum, Yaxha, and Ixlu. Hieroglyphic evidence suggests that several of these centers were either allied with or under the political sway of Tikal, but the large populations of these centers would likely have required the use of a sizeable portion of their own territorial resources.

The Voronoi diagram, also known as a Thiessen polygon, has been used as a tool in archaeological settlement analysis in many parts of the world, including the Maya area (21). Although far from precise, this method has been widely used to approximate the positions of intersite boundaries and zones of likely political economic jurisdiction. A primary limitation of earlier versions of Thiessen polygons has been that the method required each geographic center to have an equal amount of influence, whereas in fact the relative political power of individual centers was often unequal. Although solutions to this obstacle have been suggested for many years (22), the application of a weighted Voronoi polygon model, as presented here, has only recently begun to be practical because of the increased processing speeds of computer systems and running geographic software programs. In our study, a Geographic Information System was used to produce a weighted Voronoi diagram to estimate the projected boundary of Tikal's economic extraction area. In a weighted Voronoi diagram, the weight of the Euclidean distance from each point in relationship to all other points determines the boundary of each center. Tikal was given a two-thirds to one-third weight over its neighbors, thus allowing Tikal to have a greater influence on positioning territorial boundaries than any of its neighbors based on the rationale noted earlier.

**Palynological Data.** Pollen data from Lake Petén Itza (23), a deep lake that is downwind and less than 5-km south of the extractive zone of Tikal, were evaluated to assess the amount of upland forest clearance during the LCP. Pollen taxa characterizing high forest, such as Moraceae and Urticaceae, dropped to low levels during the LCP (Zone 3 of the Petén Itza core). The drop in high forest taxa is indicative of extensive forest clearance in the range of 60–70% in the Lake Peten Itza watershed based on palynological and sediment data. Additionally, taxa indicating disturbance, such as *Ambrosia* and other Asteraceae pollen, reach high percentages in this zone. Pollen results were based on percentages of arboreal pollen versus nonarboreal pollen.

Forest clearance co-occurred with erosion of sediments of low organic content, indicating high siltation rates in the watershed. Increases in K and Fe suggest greater presence of clays, and an increase in magnetic susceptibility indicates erosion of clastic material into the lake during this time period (24). According to these results at least 60% of the upland forest was cleared during the LCP, leaving ~340 km<sup>2</sup> of forest intact within the resource extractive zone of Late Classic Tikal.

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, indicate that 37-32% of the bajo lands (at least 80 km<sup>2</sup>) were cleared for agriculture and another 175 km<sup>2</sup> remained as seasonal swamp forest (Fig. S2). The amount of land clearance in the past was calculated by comparing the modern percentage of arboreal pollen versus nonarboreal pollen (at full forestation) to the percentages of arboreal pollen, both maximum and minimum, during the LCP.

**Modern Forest Surveys.** For the purposes of this study we have divided the forests into upland and seasonal wetland (or bajo) even though the tropical forests of the northern Petén District are much more complex than this simplified dichotomy (25–27). Numerous transitional forest types exist between upland and bajo, many dominated by particular palm species, reflecting subtleties in edaphic conditions and drainage patterns. In the Landsat 7 images we used in our biomass calculations we could easily distinguish between upland and bajo forest, but finer distinctions were not possible. To compensate, our extensive surveys covered 5.95 ha of forests within the bounds of Tikal National Park and subsumed much of the upland and bajo forest variability.

**Biomass Calculations.** Satellite images, remote sensing, and Geographic Information System techniques were combined with data from forest surveys to calculate the modern biomass of the forests around Tikal and determine the extent of the various forest types within the extraction zones of the Tikal community during the Late Preclassic and Late Classic periods. A March 27, 2003, Landsat 7 ETM+ image of the study area was acquired to aid in the calculation of the above ground biomass (AGB) of modern Tikal forests.

The image was atmospherically corrected using a logarithmic residuals technique (28) to mitigate as much as possible the undesired atmospheric component in all subsequent transforms. The use of this convenient, but less-exact, ad hoc atmospheric calibration technique was preferred over a more intensive atmospheric modeling approach (e.g., FLASH) because the atmospheric data necessary for the computational models are absent in this region. The use of reflectance data will be denoted by the symbol  $\rho$  (e.g.,  $\rho_{Band}$  5).

We constructed (29) an object-based imagery analysis classification methodology for differentiating seasonal wetlands from upland tropic forest and other forms of land cover and land use at a regional accuracy with a regional accuracy of 93.5% ( $\kappa =$ 0.876). These classification data, which were constructed from the same Landsat ETM+ scene and a texturally transformed version of the experimental global Advanced Spaceborne Thermal Emission and Reflection Radiometer digital elevation model imagery, were used as a processing mask for each respective AGB model. The high accuracy of the classification reduced the potential for error because of AGB model use across the image. Once each AGB model was derived, it was calculated on regions corresponding to their respective classes.

Indices and data transforms were derived from atmospherically corrected bands of the satellite dataset. By superimposing biomass parcels from vegetation surveys onto the remote-sensing dataset and experimentally regressing AGB values against the remotely sensed variables, we were able to calculate overall AGB within each forest type. A weighted mean value for pixel values was calculated for each parcel, with overlapping pixels being proportionately weighted by their area of overlap to reduce any bias resulting from the spatial discontinuity between the parcels and the coarse 30-m pixels of the satellite dataset. Ultimately, the mean imagery dataset values were tabulated with AGB values and imported into a SPSS statistical package (v16) for regression.

The relationship between predicted and measured biomass derived from statistical bands, vegetation indices, and linear decompositions (i.e., tasseled cap transform) can differ greatly in both direction and strength between regions (30). Accordingly, separate models were experimentally determined for upland tropical forest and the bajo vegetation parcels. To determine mean AGB error, both equations were entered into ENVI 4.7 and compared back to the values for each vegetation parcel. Because vegetation parcels and pixels did not perfectly overlap, each parcel was related to an areally weighted sum of AGB values of the overlapping pixels to better assess the response of

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each modeled pixel to their overlapping parcel. Each pixel that was modeled for AGB was summed and divided by the areal extent of its respective vegetation community. From these calculations the respective error bounds for each forest type was determined.

All possible combinations of relationships between bands and variables were explored using multiple linear regression for biomass calculations of bajo forests. Initial calculations indicated a strong linear relationship when data from  $\rho_{\text{Band}}$  3 (predominantly red visible light; 0.63-0.69 µm) and the Soil-Adjusted Vegetation Index (SAVI) were combined, but the relationship was not a statistically significant one. There are inherent risks in assuming a global soil adjustment weight when attempting to model subtle local variations, which predicated dropping SAVI. A strong inverse relationship occurs between  $\rho_{\text{Band}}$  3 and AGB occurs because of the preferential absorption of red light. Chlorophyll absorbs red light for photosynthesis so lower aggregate red reflection corresponds to either denser or more vigorous healthy vegetation. This relationship was most strongly indicated using a cubic curve ( $r^2 = 0.758$ , P = 0.029, n = 8, SE = 1.98) using the following equation:  $937.0139 + (-30.906)^* \rho_{Band}$  $3+0^{*} \rho_{Band} 3^{2}+0.005^{*} \rho_{Band} 3^{3}$ . A cubic relationship was used in place of a linear one not only because of the stronger statistical relationship but also because of the latter's tendency to create anomalies (e.g., large negative or improbably high values for AGB) in a way that was less predictable than the cubic curve. This model was applied only to portions of the satellite dataset indicated to be seasonal wetlands by Magee (29).

Upland forest biomass was calculated using all possible combinations of relationships between AGB, spectral bands, and derived satellite data. All were tested using multiple linear regression. Whereas previous studies have focused on the linear relationship between forest biomass and vegetation indices (31), we found the strongest relationship of the biomass of upland tropical forest to be the atmospherically corrected reflectance of one of the satellite datasets  $\rho_{Band}$  5 (sensitive to 1.55- to 1.75- $\mu m$ wavelengths). Steinenger (32) observed this same relationship for AGB estimations in tropical forests in Bolivia and Brazil. The strongest correlation between  $\rho_{Band}$  5 and each parcel's AGB, again, was found using a cubic curve ( $r^2 = 0.818$ , P = 0.006, SE = 12.02, n = 9) with the equation summarized as follows: 7428.578 +  $(-175.784)^* \rho_{Band} 5+1.041^* \rho_{Band} 5^2+0^* \rho_{Band} 5^3$ .  $\rho_{Band} 5$  has a distinct inverse relationship to the internal moisture of a plant's chloroplasts, thus providing a strong rationale for the model. Full details of the methodology of the biomass portion of our study can be found in other publications (29, 30, 33). Our findings show that the AGB of modern upland forest is 28.9  $\pm$  2.6 million kg km<sup>-2</sup> and the AGB of the bajo is  $18.2 \pm 0.523$  million kg·km<sup>-2</sup>. The results of our surveys compare favorably to data generated by biomass estimates from other Neotropical forest surveys (34).

Annual Growth Increment Calculations. The study at Barro Colorado Island (BCI) was selected as a reference to estimate annual growth increment measurements in the ancient forest at Tikal for numerous reasons: both areas are classified as moist tropical forest, both have a pronounced wet and dry season, and both are listed as having a tropical monsoon climate (Am) according to the Köppen Climate Classification System (35, 36). Both forest systems developed out of the Neotropical flora (37), which evolved in South America and then migrated into Central America when the two land masses joined together ~4 million y ago. Although the forests of Tikal and BCI are not identical in their species make-up, they share many commonalities. For example, the dominant oligarchic species in terms of basal area at Tikal is Brosimum alicastrum Sw. This is also a common species at BCI (36) and a tree whose wood is well represented among the paleoethnobotanical remains at Tikal (38, 39) (Table S2). Alternatively, the most common species at BCI

is *Trichila cipo* (A. Juss.) C. DC. Although this particular species is not found in the Tikal forests, a closely related congeneric species, *Trichila minutiflora* Standl. is one of the dominant species there (40). Three other species of *Trichila* are also found in the modern Tikal forests: *Trichila pallida* Sw., *Trichila moschata* Sw., and *Trichilia glabra* L. Parenthetically, *Trichilia* wood was identified among the archaeological plant remains at Tikal, evidence that trees of this genus were present during ancient times and of economic value to the Maya.

Although it is true that the BCI forest is in the middle of a lake and Tikal is not, that lake (Lake Gatun) is artificial and was created during the construction of the Panama Canal 100 y ago. The BCI forest was established as a result of natural processes long before the lake appeared.

Ideally speaking, the annual growth increment measurements used in this study would have come from Tikal forests or from moist tropical forests in the Petén region. Unfortunately, no longterm forest studies that generated the data that we required have been completed in the region. In short, the closest and most wellstudied moist Neotropical forest in Central America with the appropriate measurements was the BCI forest.

Ancient Wood Use. Firewood for cooking undoubtedly represented the major demand for fuel among the ancient Maya (41). Numerous ethnographic studies have recorded the daily firewood requirement of traditional Mesoamerican farmers, with the estimates ranging from 2.3 kg per person per day (42) to 3.2 kg per person per day (43). For our calculations, we used the minimum number of 2.3 kg per person per day. For 45,000 inhabitants (44), the need for cooking fuel would have been a staggering 38 million kg/yr (2.3 kg × 45,000 persons × 365 d).

Judging from Maya archaeological sites that were catastrophically destroyed (45, 46), each household would use 70–80 ceramic vessels at any given time and replace them on an annual basis because of breakage (47, 48). The ancient Maya likely used open kilns (49), which were extremely inefficient and consumed about 5.2 kg of wood per vessel (50), requiring around 73 kg per person per year (assuming five persons per family). For the entire polity of Tikal during the LCP, the total need for wood to fire ceramics was ~3.3 million kg/yr (73 kg per person per year × 45,000 persons).

Lime, along with crushed limestone, weathered limestone, and other fillers (all components of plaster) represented another major demand on the forests for fuel. Lime is made by burning crushed limestone and serves as the binder in traditional Maya plaster (51). Most of the surfaces of the site core at Tikal (including plazas, temples, palaces, ball courts, reservoirs, and causeways) were covered with plaster. This total area (620,000  $\mbox{m}^2)$ would have required 16 million kg to plaster the exterior surfaces of Late Classic Tikal. It took about 5 kg of wood to make 1 kg of lime using traditional open kiln technology (51). Therefore, it would have taken around 80 million kg of wood to plaster all of Tikal. Unlike the need for hearth fuel and firewood for ceramics, however, the demand for plaster could be spaced out over many years. Studies at Copan (41) estimated that surfaces were plastered every 50 y. If this were true at LCP Tikal then only 1.6 million kg of firewood would have been required for annual plaster manufacture and even less if the plasterers decided to "water down" the formula and use less lime in the mix.

Similar to lime production, the need for construction wood could be spread over many years, because, for example, traditional Maya houses last an average of 25 y (52). The 1778 residential structures within the central core of Tikal (53) required, according to our calculations,  $60,000 \text{ kg}\cdot\text{yr}^{-1}$ . If we double this figure to account for temples (comprised mostly of cut stone and rubble fill), scaffolding and outlying residences, then the amount of construction wood needed each year at Late Classic Tikal was

120,000 kg, a relatively insignificant figure compared with other wood needs.

The estimated annual need for fuel and construction wood for a Tikal population of 45,000 slightly exceeds what our calculations indicate was available (54) (Table S1). This shortage could have represented a challenge for the LCP Maya at Tikal. One way this shortfall could have been accommodated was the importation of pine charcoal or the cultivation of pine, as has been suggested for other Maya communities (55). Pine was widely used as a component of ceremonial activities among the ancient Maya (56, 57), but also served as an everyday fuel, especially in elite households (55). There is substantial evidence for this hypothesis at Tikal because pine charcoal was one of the most common plant remains in the paleoethnobotanical record, even though pine is not a common element of the upland or seasonal wetland forest. There is a small (180 ha) but ancient, stand (58) of pine about 20 km to the northwest of the Tikal site core that evidently was heavily exploited by the ancient Maya, but never eliminated. If the Maya were not carefully managing this resource, they easily could have wiped it out after several centuries of population growth and high demand. Conversely, it appears evident that the Maya were managing their pine and other forest resources to the optimum productive capacity.

The tree species represented in the archaeological wood assemblage are similar to the composition of tree species in the modern forests of Tikal. For example, 8 of the 10 most common hardwood trees represented in the paleoethnobotanical recordthat is, Manilkara zapota (L.) Royen, Haematoxylon campechianum L., Pouteria sp., Brosimum alicastrum Sw., Pseudolmedia glabrata (Liebm.) Berg., Nectandra sp., Protium copal (Schiltdl. & Cham.) Engl., and Lonchocarpus sp.-are among the modern forest oligarchic species (trees with high importance value based on basal area and relative stem density). The other two most common hardwood trees from the archaeological remains, Aspidosperma sp. and Licaria sp., although not oligarchic species, were frequently encountered in survey plots of the modern forests. Further evidence that oligarchic tree species were prominently represented in the paleoethnobotanical record, is that they were significantly present in greater numbers than the overall mean  $(X_{1,177} = 3.87, P = 0.049)$ , whereas the mean abundance of nonoligarchic woods among archaeological samples was not significantly different from the overall mean ( $X_{1, 177}^2 = 0.125, P = 0.72$ ). When species found in both ancient and modern contexts only were compared, the relative species abundance in the archaeological wood remains correlated positively with the importance value of woods found in the modern forest (Spearman's  $\rho =$ 0.292, P = 0.045, n = 46). These results indicate that the ancient Tikal Maya were actively selecting long-lived forest dominants for use, but did so in a way that did not perceptibly alter the forest structure. Compare this approach to the historic practice of mahogany exploitation in Belize, where a once common tree is now a rare species (59).

Although the pollen record indicates that the Late Classic Maya of Tikal reduced their upland forests by about 60%, Maya ethnographic accounts suggest that the remaining woodlots could have been protected as ancestral forests. Possibly these forests were managed using a harvesting technique, such as selective or "umbrella" felling that was used in the Middle Ages in northern Europe to preserve species diversity (60).

The idea that the Maya were managing their forests is a concept that has been presented elsewhere. Lentz and Hockaday (61) demonstrated that the monumental construction at Tikal required specific highly valued deciduous hardwoods. Timbers from trees of considerable girth were used in the construction of several of the major temples during the 8th century, long after the population boom of the LCP began. These trees could only have come from old-growth forests that were somehow protected from the heavy demand for prime agricultural land. The girth of these temple timbers declined toward the end of the 8th century, however, indicating an attenuation of the conservation practices that protected the old-growth forests for many generations. Another study (62) concluded that the Maya in the coastal area of Belize were managing their forests to maintain their major fuel source for the salt production industry.

**Agriculture at Tikal.** To understand how the vegetated environment might have been managed at Tikal, we turned to the ancient Maya village of Cerén that was covered by volcanic ash near the beginning of the LCP in A.D. 650 (45). As a result of the excellent preservation at Cerén, we know what plants the Maya were growing and also how the Maya inhabitants were growing them. Because of the overlap in cultigens used at Tikal and Cerén and the cultural similarities between the two communities, it seems likely that their agricultural practices would be analogous. Accordingly, Cerén serves as an excellent model to help interpret land use activities at Tikal.

In addition to farming activities in upland areas, which relied on annual crops, orchard trees, and root crops, our studies show that deep, cumulic soils on foot and toe-slopes surrounding bajos were also of agricultural importance. Excavations at the small settlement near Aguada de Terminos in Bajo de Santa Fe (Fig. S6) revealed that the ancient Maya occupants were indeed practicing maize and root crop agriculture in the bajos and were constructing terraces to conserve soil and water resources. The small pond adjacent to the site provided a consistent supply of water and enabled the residents to survive through the drought and into the Postclassic period.

**Stable Carbon Isotopes.** Stable carbon isotopes in the soil organic matter have been shown to hold a record of past vegetative histories where  $C_3$  forest trees and vines have been replaced by  $C_4$  tropical grasses, such as maize. Woody plants use a  $C_3$  photosynthesis pathway that is highly discriminatory toward heavy  ${}^{13}CO_2$ . Maize and other  $C_4$  grasses are much less discriminatory toward the heavier  ${}^{13}CO_2$ . Others (63–65) have demonstrated that increases in  ${}^{13}C$  in the soils organic matter provides evidence that soil pedons once hosted maize and other  $C_4$  plants associated with forest clearance for agricultural use. Soil pedons 1 through 4 (Fig. 2) were collected by bucket auger at locations between 500- and 800-m south and west of the Perdido reservoir. Augured soil samples are highly disturbed and we were unable to observe the soil laminations found in a pit located about 100-m south of the reservoir outlet.

The soil samples were collected at 15-cm depth intervals from the surface to bedrock or to a maximum depth of 195 cm. The samples were crushed, sieved (<2 mm), and homogenized. Subsamples (2 g) were further ground and sieved to less than 0.25 mm before acidification to remove carbonate and alkaline

- Garrison T, Dunning NP (2009) Settlement, environment, and politics in the San Bartolo – Xultun Territory, El Peten, Guatemala. Lat Am Antig 20(4):525–552.
- 2. Martin S, Grube N (2008) Chronicle of the Maya Kings and Queens (Thames and Hudson, New York).
- Ricketson OG (1937) Uaxactun, Guatemala, Group E 1926–1931. Part 1: The Excavations. Carnegie Institution of Washington Publication No. 477 (Carnegie Institution, Washington, DC).
- 4. Valdes JA (1986) Uaxactun: Recientes investigaciones. Mexicon 7(6):125-128.
- Rice DS, Rice PM (1981) Muralla de Leon: A lowland Maya fortification. J Field Archaeol 8(3):271–288.
- Cabrera T (2000) Resultados preliminares de las investigaciones realizadas en el Grupo Maler, Yaxha, Petén. XIII Simposio de Investigaciones Arqueológicas en Guatemala, 1999, eds Laporte JP, et al. (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 354–373.
- Hermes B, Calderón Z (2003) La secuencia de ocupación prehispánica en Nakum: Una visión preliminar. XVI Simposio de Investigaciones Arqueológicas en Guatemala, 2002, eds Laporte JP, et al. (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 305–319.
- Saturno WA, Stuart D, Aveni AF, Rossi F (2012) Ancient Maya astronomical tables from Xultun, Guatemala. Science 336(6082):714–717.

pyrophosphate extraction to remove fulvic and humic acid fractions of the soil organic matter. Carbon isotope ratios of the residual humin fraction were determined by isotope ratio mass spectrometer coupled with an elemental analyzer (63–65).

Tikal Population. To provide an accurate representation of the resource requirements of Tikal during the LCP, we needed some idea of the number of its inhabitants. Fortunately, archaeologists have addressed this subject and, using various datasets and interpretations, have estimated the population of Tikal as 45,000 (44), 62,000 (54), 80,000 (66), and 100,000-200,000 (67). The results of our research strongly indicate that the larger population estimates cited by Culbert et al. (54), Dickson (66), and Harrison (67) could not have been supported in any sort of sustainable land-use system without significant input of food and fuel from outside of the Tikal extractive zone. Note that the population estimate of 62,000 offered by Culbert et al. (54) is for the site core of 120  $\text{km}^2$  only. The entire realm of Tikal, they state, included 1,963  $\text{km}^2$  and a population of 425,000. This larger population figure, in our viewpoint, would have been impossible given the agricultural potential and fuel producing technology of the time. Some scholars have proposed the idea that major amounts of foodstuffs could have been moved from one area in the ancient Maya realm to another (68), but others (69, 70) have discounted this possibility, mostly because of the energetic constraints of moving supplies by human porter without the aid of draft animals, wheeled vehicles, or accessible waterways.

**Drought.** Other, less-densely populated communities with more consistent water supplies near Tikal were able to survive through the 9th century drought. A small household near the Aguada de Terminos, several kilometers east of the site core of Tikal, persisted and continued its occupation into the Postclassic period, long after the city center was abandoned. El Zotz, Tikal's near neighbor to the west, with a huge oversized reservoir and small population also was able to endure the drought into the Postclassic period. Both of these communities were able to survive because they had reliable water sources and small populations that did not stretch the carrying capacity of their landscape beyond its point of resilience to fluctuations in climate.

**Anthropogenic Influences.** Recent climate modeling studies in Neotropical areas (71–73) have concluded that deforestation will result in a reduction of somewhere between 5% and 30% of late wet season precipitation. This reduction is caused by reduced evapotranspiration from less vegetation and increased surface heating that results in high pressure zones in the atmosphere, which in turn disrupt convection and, ultimately, rainfall cycles. Even partial forest removal as proposed herein can contribute to this effect.

- Morley SG (1937) Inscriptions of the Peten, Vol. 1. Publication No. 437. (Carnegie Institution of Washington, Washington, DC).
- Bullard W (1960) The Maya settlement pattern in northeastern Peten, Guatemala. Am Antiq 25(3):355–372.
- Fry RE (2003) The peripheries of Tikal. Tikal: Dynasties, Foreigners and Affairs of State, ed Sabloff JA (SAR Press, Santa Fe, NM), pp 143–170.
- Fry RE (1969) Ceramics and settlement in the periphery of Tikal. PhD thesis (University of Arizona, Tucson, AZ).
- Puleston DE (1973) Ancient Maya settlement patterns and environment at Tikal, Guatemala: Implications for subsistence models. PhD. thesis (University of Pennsylvania, Philadelphia, PA).
- Puleston DE (1983) The Settlement Survey of Tikal. Tikal Report No.13. (Univ Museum Publications, Philadelphia, PA).
- Quintana O, Noriega R (2006) Tikal y sus vecinos: Complejodad cultural en el triángulo Yaxha-Nakum-Naranjo. XIX Simposio de Investigacioies Arqueológicas en Guatemala, 2004, eds Laporte JP, et al. (Museo Nacional de Arqueología e Etnología, Guatemala City, Guatemala), pp 333–339.
- Quintana O, Wurster W (2001) Ciudades Mayas del Noreste del Petén, Guatemala: Un estudio urbanístico comparativo. AVA – Materialien 59 (Philipp von Zabern, Mainz am Rhein, Germany).

- Ford A (1986) Population Growth and Social Complexity: An Examination of Settlement and Environment in the Central Maya Lowlands (Univ of Arizona Press, Tempe, AZ).
- Lou B (1997) Chalpate: Análisis del asentamiento y orientación de una centro satellite de Tikal. X Simposio de Investigaciones Arqueológicas en Guatemala, 1996, ed LaPorte EH (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 373–380.
- Fialko V (2000) Recursos hidraulicos en Tikal y sus periferias. XIII Simposio de Investigaciones Arqueológicas en Guatemala, 1999, eds Laporte JP, et al. (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 556–565.
- Fialko V (2005) Diez años de investigaciones arqueológicas en la Cuenca del Rio Holmul, region norteste del Petén. XVIII Simposio de Investigacioies Arqueológicas en Guatemala, 2004, eds Laporte JP, et al. (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 244–260.
- 21. Montmollin OD (1988) Scales of settlement study for complex societies: Analytical issues from the Classic Maya area. *J Field Archaeol* 15(2):151–168.
- 22. Boots BN (1980) Weighting Thiessen polygons. Econ Geogr 56(3):248-259.
- 23. Islebe GA, et al. (1996) A Holocene vegetation history from lowland Guatemala. *Holocene* 6(3):265-271.
- Curtis JH, et al. (1998) A multi-proxy study of Holocene environmental change in the Maya Lowlands of Petén, Guatemala. J Paleolimnol 19(2):139–159.
- Kunen JL, et al. (2000) Bajo communities: A case study from the central Petén. Cult Agric 22(3):15–31.
- Schulze MD, Whitacre DF (1999) A classification and ordination of the tree community of Tikal National Park, Petén, Guatemala. Bulletin of the Florida Museum of Natural History 41(3):169–297.
- Dunning N, Beach T, Luzzadder-Beach S (2006) Environmental variability among Bajos in the Southern Maya Lowlands and its implications for ancient Maya civilization and archaeology. *Pre-Columbian Water Management*, eds Lucero L, Fash B (Univ of Arizona, Tempe, AZ), pp 111–133.
- Green AA, Craig MD (1985) Analysis of aircraft spectrometer data, with logarithmic residuals. Proceedings of the Airborne Imaging Spectrometer Data Analysis Workshop, eds Vane G, Goetz A (Jet Propulsion Laboratory, Pasadena, CA), pp 111–119.
- 29. Magee KS (2011) Segmentation, object oriented applications for remote sensing land cover and land use classifications. PhD thesis (Univ of Cincinnati, Cincinnati, OH).
- Foody GM, Boyd DS, Cutler MEJ (2003) Predictive relations of tropical forest biomass from Landsat TM data and their transferability between regions. *Remote Sens Envi*ron 85(4):463–474.
- Zheng D, et al. (2004) Estimating aboveground biomass using Landsat 7 ETM+ data across a managed landscape in northern Wisconsin, USA. *Remote Sens Environ* 93(3):402–411.
- Steininger MK (2000) Satellite estimation of tropical secondary forest above-ground biomass: Data from Brazil and Bolivia. Int J Remote Sens 21(6-7):1139–1157.
- Lentz DL, Dunning NP, Scarborough VL, eds. (2014) Tikal: Paleoecology of an Ancient Maya City (Cambridge Univ Press, Cambridge, UK), in press.
- DeWalt SJ, Chave J (2004) Structure and biomass of four lowland Neotropical forests. Biotropica 36(1):7–19.
- Akpinar-Ferrand E, Dunning NP, Lentz DL, Jones JG (2012) Aguadas as water sources at southern Maya lowland sites. Anc Mesoam 23(1):85–101.
- 36. Croat TB (1978) Flora of Barro Colorado Island (Stanford Univ Press, Stanford, CA).
- Greller AM (2000) Vegetation in the floristic regions of North and Central America. *Imperfect Balance*, ed Lentz DL (Columbia Univ Press, New York), pp 39–87.
- Moholy-Nagy H (2003) The Artifacts of Tikal: Utilitarian Artifacts and Unworked Material (University Museum, Univ of Pennsylvania, Philadelphia, PA).
- Pohl M, Pope K, Jones J (2000) Base agrícola de la civilización Maya de las Tierras Bajas. XIII Simposio de Investigaciones Arqueológicas en Guatemala, eds Laporte JP, et al. (Museo Nacional de Arqueología y Etnología, Guatemala City, Guatemala), pp 258–267.
- Thompson KM (2013) Biodiversity in forests of the ancient Maya lowlands and genetic variation in a dominant tree, *Manilkara zapota* (Sapotaceae): Ecological and anthropogenic implications. PhD thesis (University of Cincinnati, Cincinnati, OH).
- Abrams EM, Rue DJ (1988) The causes and consequences of deforestation among the prehistoric Maya. Hum Ecol 16(4):377–395.
- Romero JJ (2003) Leña y Carbón. MA thesis (Universidad de San Carlos de Guatemala, Guatemala City, Guatemala).
- Breedlove DE, Laughlin RM (2000) The Flowering of Man: A Tzotzil Botany of Zinacantan (Smithsonian Institution, Washington, DC).

- Haviland WA (1970) Tikal, Guatemala and Mesoamerican urbanism. World Archaeol 2(2):186–198.
- Sheets P, et al. (2012) Ancient manioc agriculture south of the Cerén village, El Salvador. Lat Am Antiq 23(3):259–281.
- Inomata T, Triadan D (2010) Burned Palaces and Elite Residences of Aguateca: Excavations and Ceramics (Univ of Utah Press, Salt Lake City).
- Arnold PJ, III (1991) Domestic Ceramic Production and Spatial Organization: A Mexican Case Study in Ethnoarchaeology (Cambridge Univ Press, Cambridge, UK).
- Nelson BA (1991) Ceramic frequency and use-life. Ceramic Ethnoarchaeology ed Longacre WA (Univ of Arizona Press, Tucson), pp 162–181.
- Culbert TP (2003) The ceramics of Tikal. Tikal: Dynasties, Foreigners, and Affairs of state –Advancing Maya Archaeology, ed Sabloff JA (School of American Research, Santa Fe, NM), pp 47–82.
- Arnold DE (2008) Social Change and the Evolution of Ceramic Production and Distribution in a Maya Community (Colorado Univ Press, Boulder, CO).
- 51. Wernecke DC (2008) A burning question: Maya lime technology and the Maya forest. *J Ethnobiol* 28(2):200–210.
- Vogt EZ (1969) Zinacantan: A Maya Community in the Maya Highlands of Chiapas (Belknap Press, Cambridge, MA).
- Arnold JE, Ford A (1980) A statistical examination of settlement patterns at Tikal, Guatemala. Am Antiq 45(4):713–726.
- Culbert TP, Levi LJ, Cruz L (1990) Lowland Maya Wetland Agriculture: the Rio Azul Agronomy Program. Vision and Revision in Maya Studies, eds Clancy FS, Harrison PD (Univ of New Mexico Press, Albuquerque, NM), pp 115–124.
- Lentz DL, Yaeger J, Robin C, Ashmore W (2005) Pine, prestige and politics of the Late Classic Maya at Xunantunich, Belize. *Antiquity* 79(305):573–585.
- Morehart CT, Lentz DL, Prufer KM (2005) Wood of the Gods: The ritual use of pine (Pinus spp.) by the ancient lowland Maya. Lat Am Antig 16(3):255–274.
- Morehart CT, Helmke CGB (2008) Situating power and locating knowledge: A paleoethnobotanical perspective on Late Classic Maya gender and social relations. Am Anthropol 18(1):60–75.
- Dvorak WS, Hamrick JL, Gutiérrez JL (2005) The origin of Caribbean pine in the seasonal swamps of the Yucatán. Int J Plant Sci 166(6):985–994.
- 59. Thomson P (2004) Belize: A Concise History (Macmillan, Oxford).
- Schulze ED, Beck E, Muller-Hohenstein K (2002) *Plant Ecology* (Springer, Heidelberg).
  Lentz DL, Hockaday B (2009) Tikal timbers and temples: Ancient Maya agroforestry
- and the end of time. J Archaeol Sci 36(7):1342–1353.
- 62. Robinson M, McKillop H (2014) Fuelling the ancient Maya salt industry. *Econ Bot* 68(1):96–108.
- 63. Webb EA, Schwarcz HP, Healy PF (2004) Carbon isotope evidence for ancient maize agriculture in the Maya lowlands. J Archaeol Sci 31(8):1039–1052.
- Burnett RL, et al. (2012) The ancient agricultural landscape of the satellite settlement of Ramonal near Tikal, Guatemala. Quat Int 265(28):101–115.
- Burnett RL, et al. (2012) Upland and lowland soil resources of the ancient Maya at Tikal, Guatemala. Soil Sci Soc Am J 76(6):2083–2096.
- Dickson BD (1980) Ancient agriculture and population at Tikal, Guatemala: An application of linear programming to the simulation of an archaeological problem. Am Antiq 45(4):697–712.
- Harrison PD (1999) The Lords of Tikal: Rulers of an Ancient Maya City (Thames and Hudson, New York).
- Pyburn KA (1998) The Albion island settlement pattern project: Domination and resistance in Early Classic northern Belize. J Field Archaeol 25(1):37–62.
- Drennan RD (1984) Long-distance movement of goods in the Mesoamerican Formative and Classic. Am Antig 49(1):27–43.
- Webster D (2002) The Fall of the Ancient Maya: Solving the Mystery of the Maya Collapse (Thames and Hudson, New York).
- Kennett DJ, et al. (2012) Development and disintegration of Maya political systems in response to climate change. Science 338(6108):788–791.
- Cook BI, et al. (2012) Pre-Columbian deforestation as an amplifier of drought in Mesoamerica. Geophys Res Lett 39(16):L16706.
- Demarest AA, Rice PM, Rice DS (2005) The terminal classic in the Maya lowlands. The Terminal Classic in the Maya Lowlands: Collapse, Transition, and Transformation, eds Demarest AA, Rice PM, Rice DS (Univ of Colorado Press, Boulder, CO), pp 545–572.

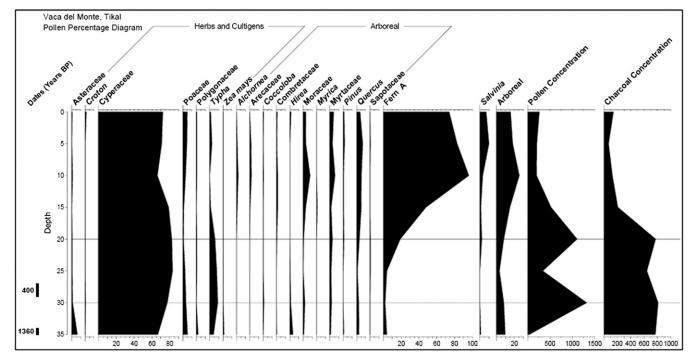


Fig. S1. Vaca de Monte pollen profile.

Late Classic Tikal Land Use Total = 1,100 km<sup>2</sup>

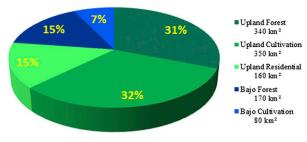


Fig. S2. Land use at Late Classic Tikal. Chart showing relative proportions of land use categories within the Tikal extractive zone.

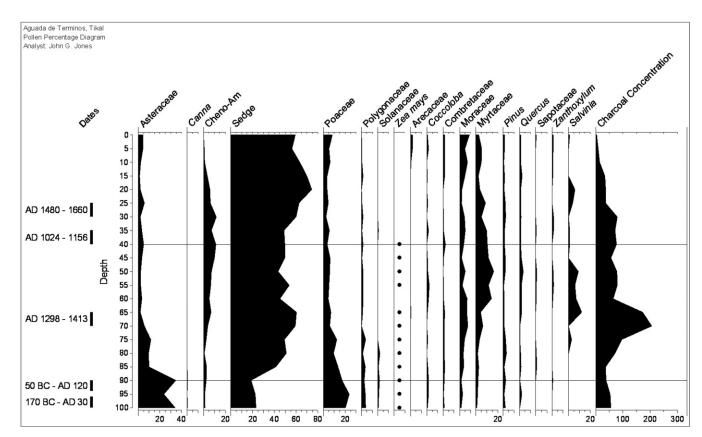


Fig. S3. Pollen profile from Aguada de Terminos. Located in the Bajo Santa Fe, just east of the site core of Tikal. Note that pollen evidence for the root crop achira (*Canna cf indica*) can be found in the earlier levels and that maize pollen is evident well into the Postclassic period.

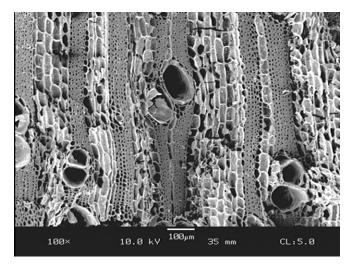
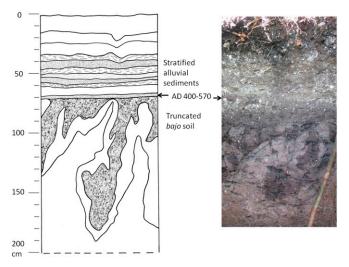


Fig. S4. Scanning electron microscopy of burned cacao (Theobroma cacao L.) wood. This micrograph provides evidence that cacao was cultivated at Tikal.



**Fig. S5.** Perdido Pocket Bajo soil profile. This is the south profile of an excavation in the Perdido Pocket Bajo (Op 8D) located just to the south of and stratigraphically below the Perdido Reservoir. The initiation of irrigated agriculture likely commenced with the radiocarbon-dated layer [cal A.D. 485  $\pm$  85 (SD)] at the bottom of the stratified alluvial sediments. Because the size of the pit from which the profile was recorded was quite small (1 m  $\times$  1 m), the photograph on the right side was taken from the ground surface, causing the lower levels of the pit to appear compressed in the image (i.e., the drawing is true to scale but the photograph is not).

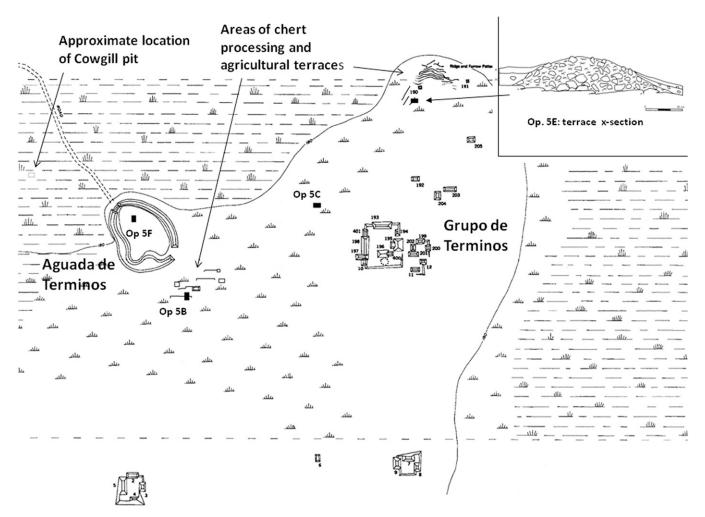


Fig. S6. Aguada de Terminos map. Note the agricultural terraces and the proximity to the bajo. The aguada, although small, is a consistent source of water and undoubtedly enabled the occupants of the Grupo de Terminos to survive the 9th century dry period. The base map is from Puleston (14), courtesy of the University of Pennsylvania Museum of Archaeology and Anthropology.

## Table S1. Fuel and timber needs of Tikal during the LCP

Quantity required (in millions of  $kg \cdot yr^{-1}$ )

Wood use	LCP population 45,000	LCP population 62,000	
Firewood for cooking	37.8	52.1	
Ceramic manufacture	3.3	4.6	
Plaster production	1.6	1.6	
Construction	0.1	0.1	
Total	42.8	58.4	

The wood needs of 45,000 inhabitants at Tikal would have stressed the system, but was potentially manageable. When we compare the wood needs of a hypothesized LCP population of 62,000 (54), it becomes readily evident that the landscape could not have supported a population of that magnitude. Total amount of wood available per year from upland and wetland forest = 39 million kg·yr<sup>-1</sup>.

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# Table S2. Ancient plant remains identified at Tikal

## Plant taxa

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Contextual data

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Annual crops [common name]	
Cucurbita moschata (Lam.) Poir. [squash]	C4;H3-4;N1;P2* <sup>,†</sup>
Cucurbita pepo L. [pumpkin]	C3;H3-4;N3;P2*
Gossypium hirsutum L. [cotton]	C3;H3;N1;P2*
Phaseolus coccineus L. [scarlet runner]	C2-3;H3-4;N2;P2
Phaseolus lunatus L. [lima bean]	C3;H3-4;N2;P2*
Phaseolus vulgaris L. [common bean]	C3;H3-4;N2;P2*
Zea mays L. [maize]	C3-6;H3-4;N33;P2,6,7,8
ree crops [common name]	
Acrocomia aculeata Lodd. ex Mart. [coyol]	C2-4;H3;N1;P4*
Bactris major Jacq. [biscoyol]	C3;H2,3;N2;P3,6
Byrsonima crassifolia (L.) H.B.K. [nance]	C2-6;H3;N2;P1,3*
Persea americana Mill. [avocado]	C5;H3;N1;P3*
Pouteria sapota (Jacq.) Mre. & Strn. [sapote]	C4;H1,3;N1;P1
Spondias spp. [jocote]	C2-5;H1,3;N8;P1,3*
Theobroma cacao L. [cacao]	C3-5;H3;N4;P1,2*
Root crops [common name]	
Canna cf indica L. [achira]	C2;H2;N1;P8
Ipomoea batatas (L.) Lam. [sweet potato]	C1;H3,4;N1;P5
Xanthosoma sagittifolium (L.) Schott. [malanga]	C4,5;H3,4;N1;P5* <sup>,‡</sup>
Other useful plants [common name]	
Cyperus canus J. Presl & C. Presl. [tule]	C4;H2;N1;P9*
<i>cf Morinda</i> sp. [pinuela]	C3;H3;N1;P1
Piper sp. [cordoncillo]	C3;H1;N2;P1
Tecoma stans (L.) H.B.K. [flor amarilla]	C3,4;H3,5;N1;P1
Thevetia ahouai (L.) A. DC. [cocheton]	C2;H1;N1;P2
rees [common name]	
Acacia sp. [subín]	C7;H1;N1;P1
Acosmium panamense (Benth.) Yak. [billywebb]	C3;H1;N2;P1
Alvaradoa subovata Cronquist [cortacuero]	C4,5;H5;N2;P1
Ampelocera hottlei (Standl.) Standl. [bullhoof]	C2-4;H1;N1;P1
Aspidosperma spp. [white malady]	C2-4;H1;N6;P1*
Astronium graveolens Jacq. [glassywood]	C2-4;H1;N1;P1
Brosimum alicastrum Sw. [ramón]	C2-5;H1;N8;P1,2
Caesalpinia sp. [warree wood]	C4;H1;N3;P1
Cameraria latifolia L. [white poison Wood]	C2;H2;N1;P1
cf Carapa guianensis Aubl. [andiroba]	C2,3;H1;N1;P1
Casearia sp. [café de monte]	C2;H1;N1;P1*
Ceiba pentandra (L.) Gaertn. [ceiba]	C5;H1;N1;P1
Celtis iguanaea (Jacq.) Sarg. [wild cherry]	C2-5;H1;N1;P3 <sup>+</sup>
Clusia sp. [matapalo]	C2;H1;N1;P1
Croton sp. [hierba de jabali]	C2,3;H2;N3;P1
Chrysophyllum sp. [star apple]	C2-4;H1;N2;P1
Cupania sp. [grande betty]	C3-5;H1,2;N1;P1
Enterolobium cyclocarpum (Jacq.) Griesb. [guanacaste]	C5;H1;N1;P2 <sup>†</sup>
Erythrina spp. [tiger wood]	C3,4;H3,5;N2;P1
Eugenia spp. [guabillo]	C2-4;H1;N3;P1
Ficus sp. [fig]	C3-4;H1;N2;P1*
Garcinia cf intermedia (Pittier) Hamm. [jocomico]	C5;H5;N1;P1
Gliricidia sepium (Jacq.) Steud. [madre de cacao]	C4;H2;N2;P1
Guarea glabra Vahl [cedrillo]	C2-4;H1;N1;P1
cf Guettarda combsii Urb. [arepa]	C7;H1;N2;P1
Haematoxylum campechianum L. [logwood]	C3-6;H2;N31;P1*
Heliocarpus sp. [broadleaf moho]	C2,3;H1;N2;P1
Hirtella sp. [pigeon plum]	C2-4;H1;N1;P1
cf Lacmellea sp. [chicle dwarf]	C7;H2;N1;P1
Licaria spp. [laurelillo]	C2-4;H1-2;N8;P1
Lonchocarpus spp. [dogwood]	C2-6;H1,2;N5;P1
Manilkara zapota (L.) Royen [sapodilla]	C2-5;H1-3,N34,P1,2*
Metopium brownei (Jacq.) Urb. [poisonwood]	C4;H2;N1;P1
Nectandra spp. [timber sweet]	C2-4;H1,2;N8;P1*
Ocotea puberula (Rich.) Nees. [wakkowit]	C2-4;H1;N2;P1
Pimenta dioica (L.) Merr. [allspice]	C5;H1;N1;P2

#### Table S2. Cont.

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Plant taxa	Contextual data	
Trees [common name] cont.		
Pinus spp. [pine]	C2-5;H5;N118;P1*	
Pouteria spp. [mamey]	C2-5;H1;N20;P1	
Protium copal (Schiltdl. & Cham.) Engl. [copal]	C2-4;H1;N6;P1,2	
Pseudolmedia glabrata (Liebm.) Berg. [cherry]	C2-4;H1;N8;P1	
Psychotria sp. [night bloom]	C4;H1;N1;P1	
Salix cf chilensis Molina [willow]	C5;H2;N2;P1	
Sebastiana sp. [poison wood]	C2-4;H1;N3;P1	
Sideroxylon sp. [silion]	C2-4;H1;N6;P1	
Stemmadenia sp. [cojotón]	C2-4;H1;N1;P1	
cf Tabebuia sp. [yellow mayflower]	C4;H1;N2;P1	
Tapirira cf mexicana Marchand [tanto]	C2-4;H1;N2;P1	
Terminalia buceras (L.) C. Wright [pukté]	C3;H2;N3;P1	
Trichilia spp. [red cedar]	C3;H1;N3;P1	
Trophis spp. [white ramón]	C3-5;H1;N4;P1	
Zanthoxylum caribaeum Lam. [prickly yellow]	C2-4;H1,2;N4;P1	
Zuelania guidonia (Sw.) Britt. & Millsp. [tamai]	C2-4;H1;N1;P1	

Chronological assessments (C) are numbered as follows: 1, Middle Preclassic (1000–300 B.C.); 2, Late Preclassic (300 B.C. to A.D. 250); 3, Early Classic (A.D. 250–600); 4, Late Classic (A.D. 600–850); 5, Terminal Classic (A.D. 850–950); 6, Postclassic (A.D. 950–1150); 7, unknown date. H represents the habitat where the plant species likely originated, numbered as follows: 1, upland forest; 2, bajo; 3, kitchen garden; 4, field; 5, other. N represents the number of contexts from which the plant remains were recovered. P represents plant part, numbered as follows: 1, wood; 2, seed; 3, pit; 4, endocarp; 5, tuber; 6, stem; 7, cob; 8, pollen; 9, leaf. \*Indicates plants also found at Late Classic Cerén.

<sup>†</sup>See Moholy-Nagy (38).

<sup>‡</sup>See Pohl et al. (39).

Upland or Bajo	Proportional BA	Upland or Bajo	Proportional density
Upland		Upland	
Brosimum alicastrum	30.4	Cryosophila stauracantha	16.6
Blomia prisca	8.2	Blomia prisca	10.8
Ficus spp.	6.7	Trichilia minutiflora	10.1
Clusia spp.	5.6	Pouteria reticulata	10.0
Pouteria reticulata	5.4	Brosimum alicastrum	7.2
Manilkara zapota	5.0	Pseudolmedia glabrata	5.0
Spondias mombin	4.5	Manilkara zapota	2.2
Cedrela odorata	2.8	Sabal mauritiiformis	2.1
Forchhammeria trifoliata	2.7	Forchhammeria trifoliata	2.0
Trichilia minutiflora	2.6	Protium copal	1.9
Total (of the top 10)	73.9	Total (of the top 10)	67.9
Вајо		Вајо	
Haematoxylum campechianum	20.3	Croton billbergianus	23.9
Sabal mauritiiformis	12.3	Haematoxylum campechianum	11.6
Croton billbergianus	9.8	Cryosophila stauracantha	9.9
Cedrela odorata	8.1	Metopium brownei	6.6
Metopium brownei	6.4	Gymnanthes lucida	6.4
Cupania belizensis	5.0	Manilkara zapota	5.2
Manilkara zapota	4.1	Sabal mauritiiformis	5.0
Simira salvadorensis	2.9	Margaritaria nobilis	3.5
Gymnanthes lucida	2.6	Lonchocarpus heptaphyllus	3.3
Cryosophila stauracantha	2.3	Nectandra spp.	2.8
Total (of the top 10)	73.7	Total (of the top 10)	78.2

#### Table S3. Modern Tikal forest survey results

Most abundant species by stem density (number of trees per  $ha^{-1}$ ) and dominant species by basal area (BA =  $m^2/ha^{-1}$ ) for each habitat (6 cm diameter at breast height threshold) in our survey plots (5.95 ha). These are the oligarchic or most dominant tree species of the modern forest (40).