

Evidence disputing deforestation as the cause for the collapse of the ancient Maya polity of Copan, Honduras

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Archaeologists have proposed diverse hypotheses to explain the collapse of the southern Maya lowland cities between the 8th and 10th centuries A.D. Although it generally is believed that no single factor was responsible, a commonly accepted cause is environmental degradation as a product of large-scale deforestation. To date, the most compelling scientific evidence used to support this hypothesis comes from the archaeological site of Copan, Honduras, where the analysis of a sediment core suggested a dramatic increase in forest clearance in the Late Classic period (A.D. 600–900). By contrast, in the work presented here, the authors' analysis of a longer sediment core demonstrates that forest cover increased from A.D. 400 to A.D. 900, with arboreal pollen accounting for 59.8–71.0% of the pollen assemblage by approximately A.D. 780–980. The highest levels of deforestation are found about 900 B.C. when, at its peak, herb pollen made up 89.8% of the assemblage. A second, although less pronounced, period of elevated deforestation peaked at approximately A.D. 400 when herb pollen reached 65.3% of the assemblage. The first deforestation event likely coincided with the widespread adoption of agriculture, a pattern found elsewhere in Mesoamerica. The second period of forest clearance probably was associated with the incursion of Maya speakers into the Copan Valley and their subsequent construction of the earliest levels of the Copan Acropolis. These results refute the former hypothesis that the ancient Maya responded to their increasingly large urban population by exhausting, rather than conserving, natural resources.

archaeology | Mesoamerica | historical ecology | sustainability | palynology

Many hypotheses have been developed to explain the collapse of the southern Classic Maya polities between A.D. 790 and 950. They include environmental degradation, climate change, warfare, top-heavy political systems, and natural disasters (1, 2). In this article we follow Culbert's (3) definition of collapse as the "cessation of major architectural activities [and] the near disappearance of dated stelae," and we add to it a dramatic drop in populations around the southern lowland centers. The hypothesis that, between A.D. 600 and 900, population pressure drove the Maya to deforest their lands and thereby to instigate large-scale erosion, first proposed by Cooke (4), has gained wide acceptance as one of the primary causes of the collapse (5–11). The collapse of the great ancient city of Copan, Honduras, has been linked to deforestation using data from a pollen profile in a sediment core taken from a pond near the urban center (12–18).

Here we analyze a new core from the same location with extracted sediments that span a much longer period. The pollen profile of this sediment core reveals that the area around the Late Classic city (A.D. 600–900) was more heavily forested than that around the Early Classic city (A.D. 400–600). Our evidence indicates that, despite a rising population and shrinking land base from A.D. 600–900, the Copan Maya were skilled managers of their landscape.

The Copan Valley lies on the southeastern periphery of the Maya region. Its earliest inhabitants probably were the ancestors of the Lenca who currently live along both sides of the Honduran–El Salvadoran border (19). Some Maya may have settled in the valley as early as the second century A.D. (20), but it was not until A.D. 427 that a Maya lord, K'inich Yax K'uk' Mo', "arrived"—in the language of the inscriptions—and became ruler of Copan (8). During or soon after the reign of its 16th king, last mentioned in an inscription in A.D. 810 (21), the polity collapsed, and its population decreased dramatically. The last dated monument records an event in A.D. 822 (8).

At the site of Copan the principal occupations are the Preclassic (1300 B.C. to A.D. 100), the Protoclassic (A.D. 100–400), the Classic (A.D. 400–900), and the Postclassic (A.D. 900–1500); the Postclassic was a time following the collapse of many Maya cities (8, 22).

Researchers working in the 1980s and 1990s at Copan argued that the health of the Classic-period polity was undermined by a series of related factors. An expanding population with growing needs for food and for wood for fuel and construction would have generated pressure on the surrounding forest cover (9, 12–18). Food production on the valley floor would have been reduced by the expansion of urban constructions into some of the most fertile agricultural fields. According to this scenario, the Maya would have been driven to reduce fallow periods and deforest the hillsides in an effort to meet their immediate needs. This short-term strategy would have decreased the fertility of the soil and ultimately would have undermined the production of adequate food supplies. The high deforestation levels in the valley would have led to erosion from the hillsides and further depletion of soils (11, 12, 17). Abrams and Rue (14) predicted that not a single pine tree (the preferred wood for fuel) would have survived in the western section (the "Copan Pocket") of the Copan Valley by A.D. 800 (Fig. 1). Furthermore, Webster et al. (17) proposed that significant erosion layers found covering structures from the Late Classic period were a product of the deforestation of the Copan Pocket.

The strongest evidence for the "deforestation hypothesis" of the Copan collapse came from a sediment core extracted by David Rue from the Petapilla pond some 4.5 km from the city center (12, 13). In ideal circumstances, the sediments on the floor of a pond preserve layers of pollen and other organics in their stratigraphy. By analyzing pollen at intervals within a sediment core, scholars

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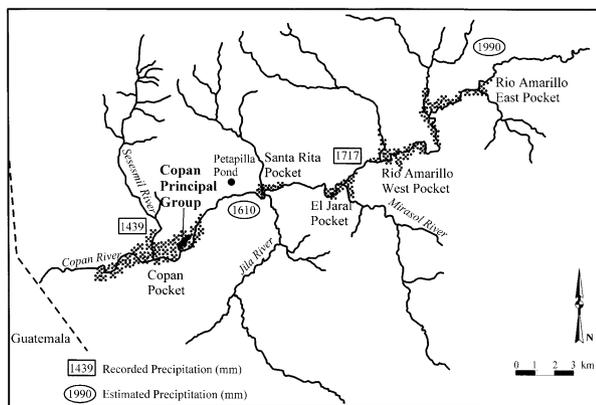


Fig. 1. Map of the Copan Valley showing its five fertile agricultural pockets (Copan, Santa Rita, El Jaral, Rio Amarillo West, and Rio Amarillo East) and their precipitation levels. (Redrawn by Timothy Pugh after Turner et al. (23) and Webster (9).

learn about the history of environmental change in the area surrounding the sampled body of water.

The oldest sediments of Rue's core date to A.D. 1010 (13), at least 100 years after the well-documented collapse of Copan's population and political system (24–26). His results were made relevant to the question of the collapse only by the revision of population estimates for the Copan Valley. These revisions, proposed by Webster and Freter (15), were based on dates obtained through a technique known as "obsidian hydration." Rejecting the notion of a more-or-less rapid collapse, the re-interpretation of Copan's settlement history instead proposed a gradual decline in population that began around A.D. 850 and ended with the final abandonment of the city in A.D. 1235 (15, 18). This reassessment of Copan's settlement history placed the earliest levels of Rue's sediment core in the middle of a long "process of collapse" (16) rather than after a collapse had occurred. Rue's analysis indicated that the area near the Copan Acropolis was still heavily deforested in the 11th century and supported the notion that the population collapse was gradual and ongoing. His data suggested deforestation had continued for perhaps 400 years after the last dated hieroglyphic inscriptions at the site, ending around A.D. 1200 with the reestablishment of a forest of *Pinus* (pine), *Quercus* (oak), and *Meliaceae* (mahogany) (12, 13, 16).

The "gradual collapse" thesis, however, is problematic because scholars have demonstrated that obsidian hydration dating, as practiced at Copan in the 1990s, incorrectly modeled the complex weathering processes undergone by the dated artifacts (27, 28). This erroneous modeling produced erroneous dates that created false indications of extended collapse (27). In addition, a slow demographic decline is not supported by other lines of archaeological evidence at the site (26, 29, 30). Thus, Rue's sediment core is from the Postclassic period and does not provide information concerning the environmental impact of human populations during the Classic period.

In 2001, McNeil (30) extracted a core from the Petapilla pond, whose oldest sediments date to $2,670 \pm 40$ ^{14}C years B.P. (900–790 calibrated years B.C. at 2σ) (β -158480). The core is intact in all but its first meter, where 50–60 cm may have been lost because of a blockage in the tube. The sediments contain an abundance of information on nearly 3,000 years of human–environmental interaction in the Copan Pocket.

Analysis of the pollen profile in the present core has produced data on Copan's environmental history that differ significantly from the data proposed by advocates of the deforestation hypothesis. Although the ratio of upland herbs to trees indicates several episodes of heightened deforestation, none of these ep-

isodes correspond to the Late Classic period (A.D. 600–900), the time of the collapse.

The most dramatic period of deforestation in the last 3,000 years was in progress by ≈ 900 –790 B.C. The earliest levels in the core (515–487 cm) are dominated by Poaceae (grasses) and Asteraceae (daisies) pollen and microscopic charcoal (Figs. 2 and 3). The highest level of deforestation is found at the 512-cm mark with 89.8% of the pollen profile made up of herb pollen (percentages in this article, unless otherwise explained, are of the combined tree, shrub, and herb pollen, not including aquatic pollen and spores). The presence of *Zea* spp. pollen from the core's earliest level may indicate that fields of maize (*Zea mays* L.) were grown near the pond, because maize pollen generally does not disperse far from its source. Although work by Holst et al. (31) has demonstrated the difficulty of distinguishing maize pollen from wild teosinte (*Zea* spp.), the association of *Zea* pollen in our sample with layers indicative of forest clearance and containing an abundance of microscopic charcoal strongly suggest an agricultural origin. Large-scale deforestation events concomitant with the presence of *Zea* spp. pollen have been found throughout Mesoamerica 3,000–4,500 years ago and indicate a transition from hunting and gathering to agriculture (13, 32–37).

There is a brief period of reforestation at 443 cm. In this level, arboreal pollen makes up 75.2% of the terrestrial pollen assemblage. A sample of peat from 443 to 442 cm yielded an accelerator mass spectrometry (AMS) date of $2,190 \pm 40$ ^{14}C years B.P. (380–160 calibrated years B.C. at 2σ) (β -175312). In subsequent levels (423–359 cm) a period of relative balance occurs between species representing forested and open spaces.

A second period of elevated forest clearance, initially manifested as an increase in Poaceae pollen, begins at 344 cm as herb pollen increases from 33.6% to 54.0% of the profile. The onset of this episode likely occurs in the Late Protoclassic period, and the episode reaches its height at the 324-cm mark, when herb pollen makes up 65.3% of terrestrial pollen. This latter episode of deforestation is less dramatic than that of the Preclassic period. The level at 344 cm also marks the first appearance of the pollen of coyol [*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.], a palm tree with a range of economic uses (Fig. 2). *A. aculeata* was an integral part of the ancient Maya subsistence base, which revolved around the consumption of foods from both fields and forests. Lentz (38) has suggested that coyol palms may have been introduced to Copan by the Maya. The first archaeological evidence of the presence of Maya in the valley is found in the 2nd century A.D. (20), although the appearance of coyol may date to a century or more later, judging from its position in the sediment core in relation to a well-dated stratigraphic marker.

The lack of stratigraphic markers, such as identifiable volcanic ash (tephra) layers, in sediment cores extracted near Maya sites has limited scholars' ability to tie ecological history to dates and events in Maya antiquity with any precision (39). AMS generally provides Classic-period dates within a 200-year range. Such a large margin of error limits the utility of sediment cores for studying the human environmental impact of the Classic period, which at Copan is at most 500 years long. The sediment core discussed here, however, contains the Tierra Blanca Joven (TBJ) tephra layer from El Salvador's Ilopango Volcano, which is found at 321.1–320.75 cm. The ash layer was identified by Andre Sarna-Wojcicki of the US Geological Survey Tephrochronology Laboratory through chemical comparison with known tephra signatures (Fig. 4). The TBJ tephra has been dated 9 times, with an overlap range of A.D. 408–536 and with the eruption most likely occurring around A.D. 430 (40). A twig fragment that rested against the upper limit of the tephra in Petapilla was dated to 1540 ± 40 ^{14}C B.P. (calibrated years A.D. 420–620 at 2σ) (β -167234). This tephra layer provides a reliable chronological marker that allows us to tie the environmental history of Copan

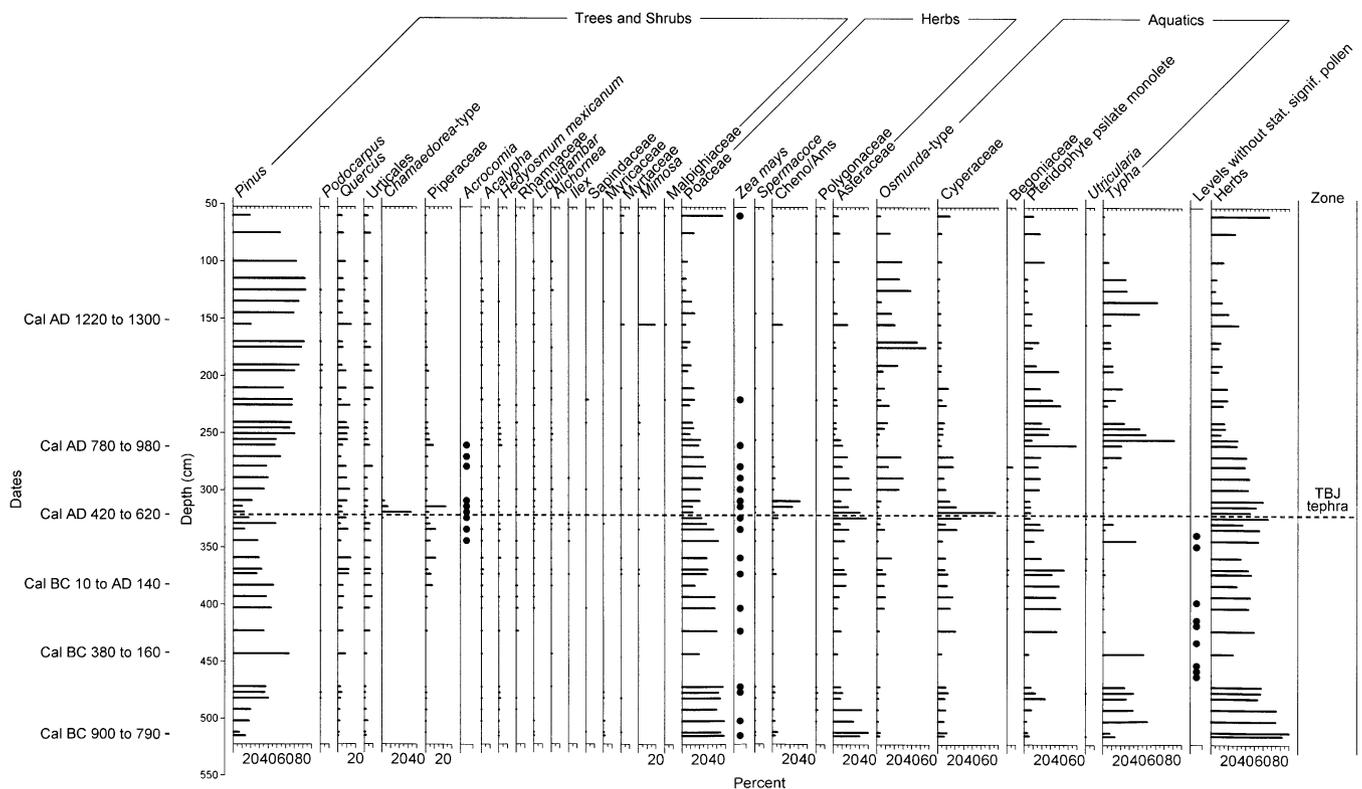


Fig. 2. Graph of pollen percentages in the Petapilla pond sediment core. Arboreal (tree and shrub) and herb percentages are of the sum of tree, shrub, and terrestrial herb pollen. Aquatic species percentages are of the sum of aquatic pollen and spores, and all terrestrial pollen. Six AMS dates are given along the left of the graph. Levels where statistical significance of pollen could not be attained are marked with dots in the second to last column on the right. The presence of *A. aculeata* and *Zea* spp. pollen is indicated by dots.

to the written history more securely than has been possible for previous researchers.

The peak of the second period of heightened deforestation occurred shortly before the eruption of the Ilopango Volcano. This peak may be a product of the arrival of the first king of the Copan Maya dynasty in A.D. 427. Excavations in the Copan Acropolis have determined that as much construction occurred in the 75 years after the king's arrival as in the following 300 years of the Classic period (22, 41). Large amounts of wood would have been required to produce stucco for the buildings and plaza floors during this episode of intense construction activity.

The heightened level of deforestation continues unevenly into the Early Classic period. A large volume of *Chamaedorea*-type (palm) pollen found immediately after the TBJ tephra layer is responsible for a brief decrease in the ratio of herb pollen to forest and shrub pollen. The conclusion that this pollen is from the palm family has been reached through discussion with other palynologists and through study of comparative samples. However, its volume and pattern are more consistent with those of aquatic species whose numbers were elevated following the deposition of the tephra. If this pollen proves to be an aquatic species, and not a palm (associated with forest regeneration), then elevated deforestation would be documented consistently from 324 to 309 cm in the sediment core.

In contrast to earlier research, analysis of the present core shows that the ratio of arboreal pollen to herb pollen in the Late Classic period is relatively stable, with a higher amount of arboreal pollen than found during the Early Classic period (Fig. 2). *Pinus* pollen, in particular, increases overall during this time, disproving predictions that the hills would have been denuded of pine trees. The increase in *Pinus* and other arboreal pollen grains may indicate that the Late Classic Maya were practicing more

controlled ecological management than they had during the Early Classic period, possibly in response to soil depletion caused by deforestation and erosion in the Preclassic and Early Classic periods. Research in Copan's center has determined that thinner layers of stucco were used on sculptured buildings during the Late Classic period than during the Early Classic period (42). Because the production of stucco requires large volumes of wood, the reduction in its use may have been one of a host of available conservation methods adopted by the Maya to preserve their resources.

Although the pressures of an increasing population may have diminished the prime farm land available in the floor of the Copan Pocket, there are signs that the polity's inhabitants may have used the larger valley and beyond to offset this loss. During the Late Classic period, the far eastern section of the valley (Río Amarillo West and East) was receiving trade goods funneled through the Copan Pocket, although it is not clear what was being exchanged for these goods (43, 44) (see Fig. 1). The Río Amarillo Pockets, which never had a large population, have the highest annual rainfall of the valley and have rich alluvial soils (23). The eastern section of the valley could have become the bread basket for the polity center, compensating for the shrinking land base. The data in the sediment core support a relatively abrupt collapse (see Fig. 2). Between 270.5 cm and 260.5 cm in the core, the percentage of arboreal pollen increases first from 59.8 to 71.0%, and then, between 255.5 cm and 250.5 cm, increases from 70.3 to 89.8%. An AMS date on a peat sample from 262.5–261.5 cm yielded a date of 1160 ± 40 ^{14}C years B.P. (calibrated years A.D. 780–980 at 2σ) (β -174808), which encompasses the last dated inscription at Copan in A.D. 822 (8). At the 250.5-cm mark, herbs (in this case, predominantly members of the Poaceae and Asteraceae families) make up only

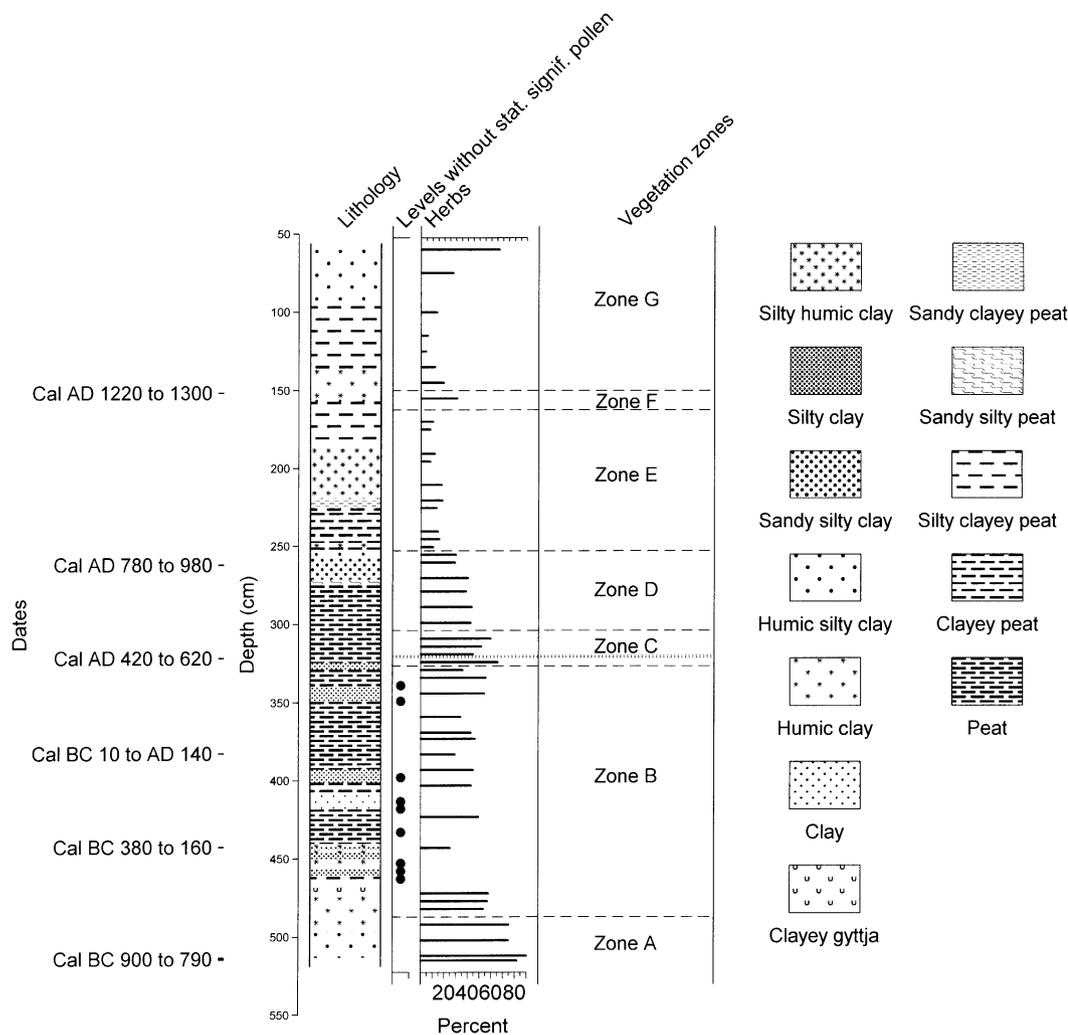


Fig. 3. Lithology and vegetation zones of the sediment core. The lithology can be found in the far left column, and the vegetation zones are delineated in the far right column. Between these two columns are columns depicting the levels with low pollen and the percentage of herb pollen vs. arboreal pollen.

10.2% of the assemblage. This rise in arboreal pollen and drop in herb pollen is extended, representing a reforestation period unparalleled in this pollen profile. During the Postclassic period, coyol ceases to be grown around the pond, *Zea* spp. pollen occurs only in one additional level at least a century later, and pine dominates the pollen assemblage. The abruptness of the end of the once-thriving city suggested by the sediment core is also marked in the archaeological record—namely, by the vandalizing and burning of the royal compound (26).

The reforestation of the area near the Acropolis does not preclude the presence of humans in the lowlands of the Copan Pocket during the Postclassic period. The *Zea* spp. pollen grains found at 220.5 cm in the sediment core likely indicate that people farmed in the area around Petapilla for at least a short time following the ancient city's collapse and may correspond to a brief reoccupation of the land around the Acropolis identified by Manahan (29) and dating to approximately A.D. 950–1100. In addition, there is a brief rise in herb pollen around 750 ± 40 ¹⁴C years B.P. (calibrated years A.D. 1220–1300 at 2σ) (β -174807) (see Fig. 2).^{*} Nonetheless, the overall increase in pine tree pollen and marked decrease in pollen from herbs indicates an environment with a dramatically reduced human population in the Postclassic period.

Even though Rue's sediment core covered the Postclassic period, his interpretations of it (12, 13) were very different from ours. Several factors are responsible for the differences between our results and his. Rue (12) grouped the majority of fern spores (which make up a significant percentage of the spore/pollen assemblage) with species indicating open space. Most fern spores in the sediments are from aquatic species and should not have been included in the ratios of forest to herb pollen. C.L.M.

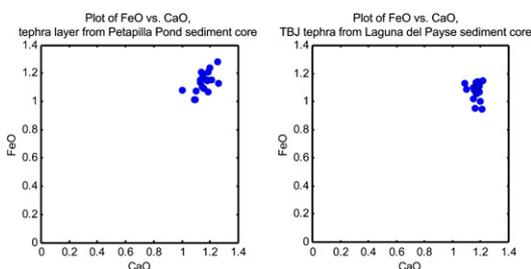


Fig. 4. Comparison of the quantity of ferrous oxide (FeO) vs. calcium oxide (CaO) in two tephra samples. The similarity in the proportions of FeO and CaO in the tephra sample from the Petapilla pond (Left) and a known TBJ tephra sample from Laguna del Payse, El Salvador (Right) indicates that the ash layer in the Petapilla pond is TBJ also.

^{*}The pollen spectrum of the 155-cm level is distinctly different from that of other sections of the sediment core. In this level, 16.1% of the pollen remains unidentified, and *Mimosa* spp. pollen accounts for 18.6% of the terrestrial pollen assemblage. Comparison of this grain with samples of *Mimosa* spp. pollen from Mesoamerica has led to the determination that it is likely to be *Mimosa albida* Humb. & Bonpl. ex Willd., a shrub.

collected pteridophyte spore samples from a fern species that carpets the Petapilla pond and determined that it was the likely source of the large amount of psilate monolete spores found in the sediments of the core described here. The second type of pteridophyte spores found in abundance in the core is *Osmunda*-type. *Osmunda* pteridophytes grow in wet habitats and also should be excluded from the forest-to-herb pollen ratio (45). The authors did not identify any Meliaceae pollen grains, which Rue (12, 13) documented as important evidence of the late return of a tropical lowland forest around Petapilla. In addition, the significantly extended time depth of the new sediment core allows comparison of the ratios of forested to open space over nearly 3,000 years and provides a more refined and precise view of human–environmental interactions in the Copan Pocket.

Pollen was not the only line of evidence used to bolster the hypothesis of Late Classic environmental degradation at Copan. Scholars additionally proposed that erosion covering Late Classic period structures was a by-product of the substantial loss of tree cover in the period leading up to (and immediately following) the collapse (16, 17). However, no systematic analysis that would support this speculation has been conducted on the deposits covering Late Classic structures throughout the Copan Pocket. It is equally likely that the “erosion” identified in conjunction with Late Classic structures is a product of taphonomic processes that occurred over the last 1,000 years or forest clearance that has occurred in the last 100 years. For example, according to local inhabitants, a series of small ponds in the Sesesmil section of the Copan Pocket were filled in by sediment within the last 50 years because of heavy deforestation.

Investigations in the Maya area have found varying patterns of erosion (37, 46, 47). Although research on erosion layers around some Maya centers has supported environmental degradation during the Late Classic period, no such evidence can be found at other centers (37). In addition, Beach et al. (37) note that, although erosion associated with initial land clearance was “pervasive,” conservation efforts in response to such land degradation also were widespread.

Evidence of erosion in the Petapilla sediment core is confined to levels earlier than the Late Classic period. Nine levels of the Preclassic, Protoclassic, and possibly Early Classic sediments do not contain statistically significant amounts of pollen (see *Methods Summary*). Seven of these sediment levels are predominantly clay, and 2 are predominantly peat (clay: 464–463, 459–458, 454–453, 419–418, 414.4–413.4, 399–398, 350–349 cm; peat: 434–433, 340–339 cm) (Figs. 2 and 3). The clay levels, in particular, may be a product of the rapid deposition of soil eroded from denuded hillsides during periods of rain and recall the “Maya Clay” layers found in lakebed sediments elsewhere in the Maya area (46, 47). The first 3 of these clay levels follow the earliest period of forest clearance preserved in the sediments when the hillsides first may have lost their vegetation (see Figs. 2 and 3).

There are data that suggest that a drought, or series of droughts, occurred at the time of the collapse (48–50). Evidence found in the Petapilla sediments and elsewhere in the Copan Valley may support a dry period at the end of the Classic period. Rue’s (12, 13) Postclassic sediment core struck “impenetrable clays” dating to approximately A.D. 1010, which could be a product of drought. McNeil (30) extracted a core from a pond above the community of Sesesmil Primera in Copan and also hit impenetrable clay layers. Leaf fragments embedded in the layers above the dense clay had a date of $1,000 \pm 40$ ^{14}C years B.P. (calibrated years A.D. 980–1060 at 2σ /calibrated years A.D. 1080–1150 at 2σ) (β -154400). Impenetrable clay layers frequently are a product of the exposure of sediments to air and thus could indicate that bodies of water in Copan either were completely dry or had extremely low levels of water during the Late Classic period. Additional support for a drought may be found in the 255.5-cm level of the sediment core where cattail (*Typha*) pollen

makes up 80.8% of the identified pollen and spore total (Fig. 2), indicating that littoral plants had moved into what today is the deepest section of the pond. Unfortunately, this conclusion is species dependent. The pollen in Petapilla is either *Typha latifolia* (shallow water cattail) or a cross of *T. latifolia* and *Typha domingensis* (deep water cattail), and a hybrid can exhibit the traits of both parents. Research into the possibility of drought at Copan during the Terminal Classic period (A.D. 780–900) is ongoing.

Although the pre-Columbian Maya once were believed to be simple swidden agriculturalists, we now know that they used a wide array of subsistence strategies (51–53). Pre-Columbian landscapes undoubtedly were composed of creatively produced plant systems including agricultural fields, raised wetland fields (51), kitchen gardens (54), terraced hills (55, 56), and—perhaps most important for our argument—managed forests (57). Modern managed forests in Maya areas (or “orchard gardens”) generally contain a diversity of useful species that provide food, medicinal plants, and firewood and attract wildlife that serve as a valuable protein food source (57–59). If the ancient Maya in Copan created such managed forests, they could have conserved their environment while still producing vital resources for the community.

For more than 20 years, the ancient Copan Maya have been held up as an example of a population that failed to practice sustainability and thus suffered a complete collapse. The results of research conducted at Copan in the 1980s have been seized upon by scholars who focus on the phenomenon of societal collapse and offered as a warning to modern populations. Perhaps most famously, Diamond (10) has used Copan as an example of short-sighted abuse of the environment, writing “Why didn’t the leaders of the Maya ... recognize and solve their problems? What were the Maya thinking while they watched loggers clearing the last pine forests on the hills above Copan?” The “fact” that the Copan Maya destroyed their environment in the Late Classic period has been accepted by many scholars in a range of disciplines, and theories of societal collapse have been rewritten to reflect this assumption. Nevertheless, the evidence presented here suggests that Copan cannot be used as a case study to demonstrate that deforestation was an important factor in the collapse of the ancient Maya cities. At the close of the city’s Classic period, the hills above Copan were more densely forested than when the Maya first built their polity center. The collapse of the ancient Maya cities may have numerous causes in common, but deforestation was not among them.

Methods Summary

The sediment core was extracted using a Livingstone Sampler with a locking piston and sampling tubes 1.5 inches in diameter constructed by Vincent Vohnout of Geo-Core. Upon extrusion, samples for pollen analysis were taken at 5-cm intervals along the upper half (horizontally) of the sediment core, leaving the lower half as a voucher specimen from which the sediment types of the core were analyzed. Samples for AMS dates were taken between the pollen samples. To begin the pollen-extraction process, 0.5 cm³ of soil was placed in a 15-mL test tube. The techniques used to extract the pollen from the sediment samples are based on the procedure set forth by Faegri et al. (60). To determine pollen concentrations, each sample was spiked with a tablet of *Lycopodium* spores obtained from Lund University, Sweden. Then the pollen was suspended in liquid glycerin. Three slides were made of each sample containing 6 drops of the pollen residue and glycerin mixture. The pollen and spores were counted and identified at 400 \times . At least 200 grains of arboreal and shrub pollen per sample (or 1,500 terrestrial grains) were counted. Pollen and spores were identified by comparison with images in atlases and by the creation of a comparative collection focused on Honduran flora.

Pollen percentages were analyzed and graphed through TILIA software (TGView created by Eric Grimm, Illinois State Museum, Springfield, IL). Percentages of pollen from trees, shrubs, and nonaquatic herbs were compared against each other. Percentages of pollen and spores from aquatic species were compared against the sum total of terrestrial pollen and aquatic pollen and spores. Pollen zones were defined using constrained cluster analysis (CONSISS) on the transformed square roots of the pollen percentages (61).

This analysis was conducted on pollen grains comprising >3% in at least 1 level of the sediment core.

Changes in the sediment types within the core were documented by making water-mount slides of sediment samples of each defined sediment type. Sediment types were assessed at 10× magnification and were determined based on the composition of organics, clay, silt, and sand. Munsell Soil Color Charts (62) were used to document changes in sediment color.

Tables containing supplementary data can be found in the *SI* in the on-line version of this publication. These tables contain raw data counts for pollen and spores (Table S1); percentages of the raw data used to create the graph in Fig. 2 (Table S2); and ^{14}C age estimates from AMS analysis (Table S3).

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