ANTHROPOLOGY

Persistent Early to Middle Holocene tropical foraging in southwestern Amazonia

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The Amazon witnessed the emergence of complex societies after 2500 years ago that altered tropical landscapes through intensive agriculture and managed aquatic systems. However, very little is known about the context and conditions that preceded these social and environmental transformations. Here, we demonstrate that forest islands in the Llanos de Moxos of southwestern Amazonia contain human burials and represent the earliest settlements in the region between 10,600 and 4000 years ago. These archaeological sites and their contents represent the earliest evidence of communities that experienced conditions conducive to engaging with food production such as environmental stability, resource disturbance, and increased territoriality in the Amazonian tropical lowlands.

INTRODUCTION

Before the 16th century European conquest, the South American Amazonian tropics witnessed the emergence of a diversity of hunting, gathering, fishing, and agricultural societies that engaged in multifaceted resource management strategies that substantially transformed plant, animal, soil, and aquatic systems at a biome scale (*1*–*5*). The Llanos de Moxos of southwestern Amazonia (section S1) was one of the regions that experienced more extensive landscape transformation as a series of agricultural societies built widespread networks of habitation and ceremonial mounds, hundreds of kilometers of causeways, and thousands of hectares of raised fields starting after 2500 calibrated years before present (cal B.P.) (Fig. 1A) (*6*–*8*). Biogeographic and genetic studies have also identified southwestern Amazonia as one of the likely hotspots where economically important cultigens such as manioc, sweet potatoes, wild rice, chili peppers, and peanuts were initially domesticated (*9*–*13*). Nevertheless, because of the taphonomic and methodological challenges involved in conducting research within a tropical environment with poor organic preservation and devoid of raw material sources for stone-based material culture, we know very little about the foraging societies that domesticated these plants and preceded the development of early food production before 2500 cal B.P. (section S2) (*14*–*18*).

Here, we reconstruct the paleoenvironment, subsistence, and adaptive strategies of early Amazonian foragers by studying preceramic open-air shell midden deposits dating before the emergence of fully agricultural socio-environmental systems (*19*). Specifically, we report our findings from archaeological, bioarchaeological, and paleoecological research in three forest islands located in seasonally flooded savannas: Isla del Tesoro (SM1), La Chacra (SM3), and San Pablo (SM4). We use this information to reconstruct the foraging behavior, landscape management, and resource utilization strategies of early tropical hunter-gatherers in southwestern Amazonia.

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RESULTS

Stratigraphic and cultural contexts

Isla del Tesoro (SM1) is a circular forest island that covers approximately 1200 m^2 (Fig. 1B). Previous radiocarbon dating and stratigraphic analysis including the identification of diagnostic anthropogenic lipid biomarkers (such as coprostanol steroids) and micromorphological signatures of human activity (such as burned and fragmented woods, shells, and bones) suggest that the site was formed through successive buildup of shell midden layers between 10,600 and 4000 years ago (*19*). Our subsequent archaeological excavations, totaling 5 m^2, verified that the site was formed by multiple overlapping layers of gastropod shells, animal bones, and burned earth (Fig. 2). Moreover, at 1.3 m beneath the surface of the site, covered by a series of compact layers of shells, and right above the water table, we identified a human burial. The skeleton was fully extended, in prone position, and embedded in a layer of well-preserved gastropod shells. We were not able to directly date the human bones because they were covered in carbonates and collagen preservation was poor. Nevertheless, two concordant charcoal samples from the overlying layer provide a minimum age of 6300 cal B.P..

Before the Late Holocene, the ancient landscape surrounding SM1 was very different from the grassland savanna surrounding it today. A paleosol largely contemporary with the early human occupation suggests that the shell midden formed during a period of environmental stability (*20*). The development of the paleosol and the early human occupation was interrupted by the deposition of 1.5 m of alluvium by a former course of the Rio Grande (*21*). This alluvium partly covered SM1 while it buried the ancient soil, and it even contributed to the formation of Lake Perotó, located a few hundred meters to the west of SM1. The modern forest island and a small ceramic occupation associated with the later Moxos agricultural deposits formed on top of the protruding shell midden.

SM3 is a circular forest island that measures approximately 3850 m^2 (Fig. 1C). We conducted two excavations at the site covering 5 m^2 and reaching 1.8 m below the surface (Fig. 2). The first stratum bears evidence of Late Holocene human occupation, including a few ceramic sherds, carbonized peach palm (*Attalea phalerata*) seeds, and fragmented bones of small mammals and reptiles including caimans (*Caiman yacare*), tegus (*Tupinambis* sp.), and armadillos (*Dasypus* sp.), which are common in tropical wetland

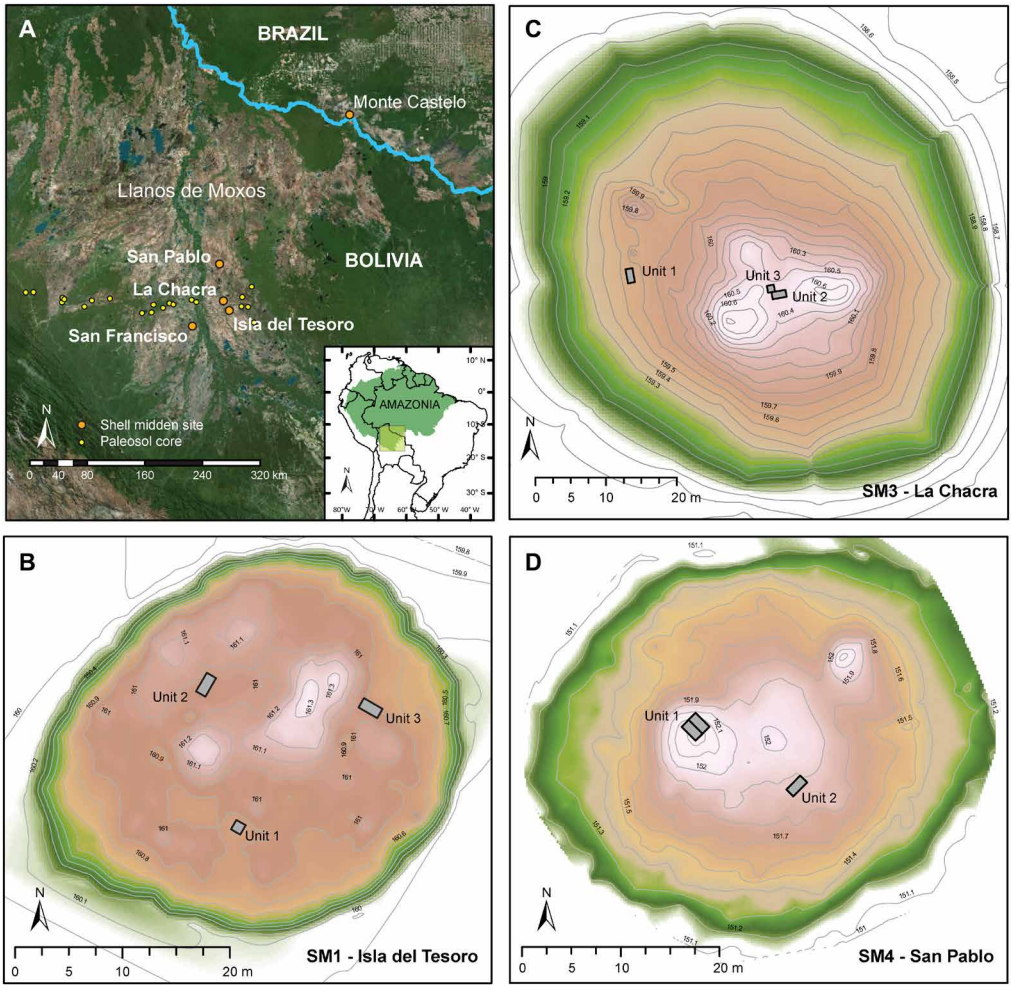

Fig. 1. Location of the Llanos de Moxos and the excavated forest islands. (**A**) Location of known shell midden sites in relation to paleosol cores containing stratigraphic evidence of buried paleosols. Topographic maps showing the excavation units at (**B**) Isla del Tesoro (SM1), (**C**) La Charca (SM3), and (**D**) San Pablo (SM4). Photo credit: (A) Base image: World Imagery, Esri.

habitats. Underneath this occupation sits a series of dark silty clay layers of alternating compact and less compact sediment. These layers have abundant remains of fragmented and pulverized shells, which enhanced carbonate precipitation of bones. Some of these deposits contain low densities of animal bones and carbon specs and medium to high densities of burned clay. Approximately 1.5 m below the surface and embedded in compacted sediment formed by pulverized shell fragments, we identified three human burials. Two of the burials were laying at the same level. The third burial was situated underneath the first burial. A charcoal sample collected from the thin layer between the second and third burial dates to 6820 cal B.P. Other human bones were occasionally mixed within the overlaying strata.

Similar to SM1, the area surrounding SM3 was buried underneath the Rio Grande sedimentary lobe. Moreover, SM3 is situated 1.5 km north of a paleochannel that, according to optically stimulated luminescence and radiocarbon dates, formed approximately 14,000 years ago but ceased in activity between 8200 and 3800 years ago (*22*). However, despite paleosols having been found in several locations below the sedimentary lobe, we did not find any paleosol in a number of sedimentary cores placed on the immediate surroundings of SM3. Therefore, the anthropogenic layers of this forest island lie almost 1 m below the current savanna, indicating that more than a meter of alluvium was deposited around SM3 after it was initially occupied.

SM4 covers approximately 1580 m^2 (Fig. 1D). The forest island is situated within an elongated waterlogged wetland surrounded by plintosols covered by cerrado-like vegetation. We excavated two units covering 6 m^2, which reached 1.63 m below the surface, and featured the identification of several occupation layers mostly dated between 7700 and 5900 cal B.P. (Fig. 2). The site's initial occupation was followed by a hiatus layer and a subsequent reoccupation during the Late Holocene by ceramic-producing agriculturalists. Unlike the deposits at the two other sites, the stratigraphic deposits at SM4 consisted mostly of burned clay and animal bones with a few shells. We documented a heavily mineralized human burial placed in an extended position and remnants of a second individual, from which we recovered a radius and ulna. A radiocarbon-dated charcoal sample from the sediment overlying the human burial suggest that it was deposited before 6250 cal B.P. In addition, we documented a large burning feature or hearth approximately 0.92 m beneath the surface in association with abundant fragmented bones of large mammals. Overall, shell remains were not as abundant in SM4 deposits as in those of the other two sites. Fragments of relatively flat and circular Planorbidae

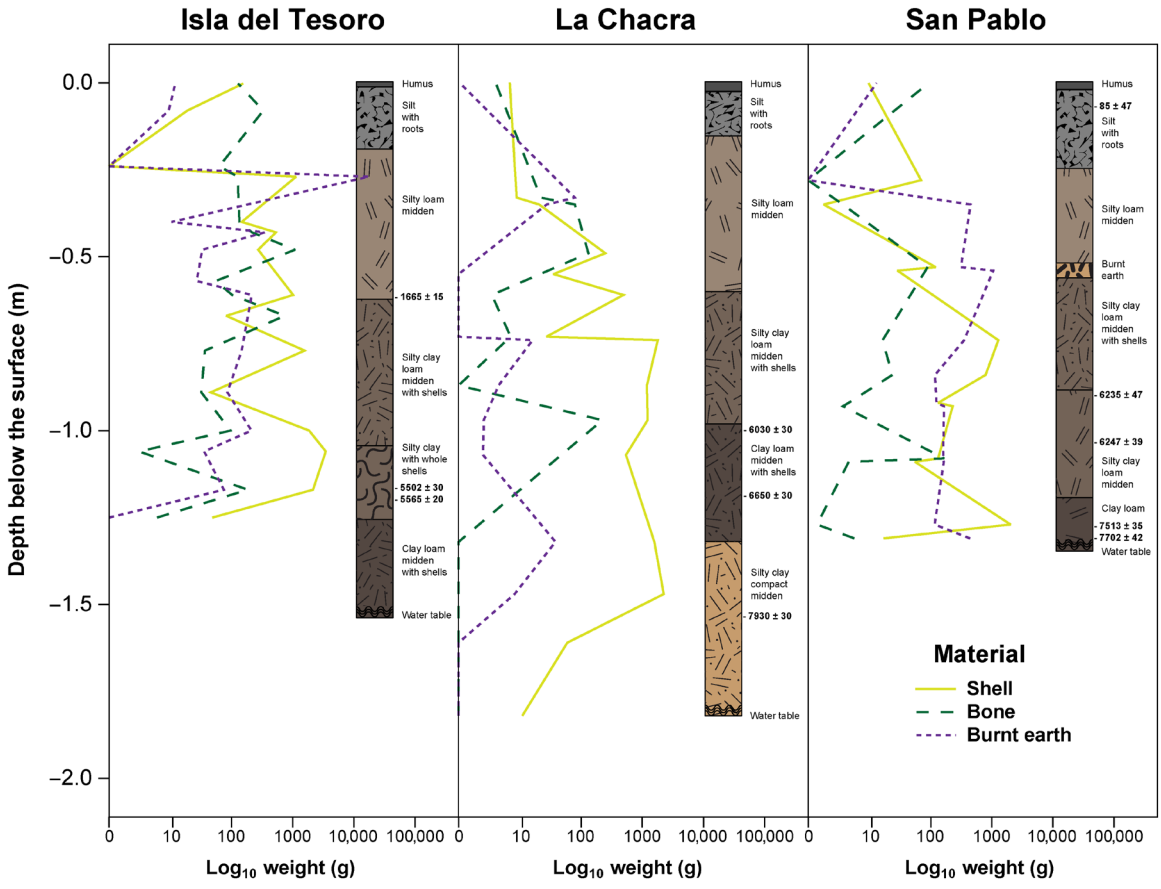

Fig. 2. Stratigraphic diagrams and calibrated radiocarbon dates in relation to weight frequencies of analyzed shell, bone, and burnt earth specimens from the study sites. Note the pattern of initial increase and subsequent decrease in the abundance of shell remains, while bones and burnt clay fluctuate over time.

shells were common in SM4 deposits, however, and indicate that people were exploiting resources from a different environment. Sedimentary cores placed within and outside the forest island suggest that SM4 formed in what seems to be a paleovalley that was later obstructed and transformed into a lake (Fig. 3). Outside the forest island, fluvial sand is covered by fine and very organic sediments, which in turn are overlaid by peat. This stratigraphic change probably marks the transition from a fluvial environment to a lacustrine one (fine organic sediments) and then to the current marsh (peat). A radiocarbon age of a paleosol found in a core situated on the northern margin of the swamp suggests that SM4 was surrounded by a shallow lake at the time it was occupied. This marks a significant contrast with SM1 and SM3, both of which were associated with the Rio Grande sedimentary lobe.

Human burials

The preservation of human burials from warm, humid, and acidic tropical depositional environments is very rare. Nevertheless, during our excavations, we recorded five human burials distributed across all three sites (Fig. 4). The basic calcium carbonate burial environment enhanced by the deposition of the gastropod shells facilitated the structural preservation of bones. However, as a consequence, all burials were heavily mineralized and encrusted by calcium carbonates. The crania in all burials were heavily affected by compression, causing fragmentation at SM1 and SM4 and taphonomic distortion at SM3. All of the documented burials included single adult individuals in horizontal extended positions albeit in a range of orientations and including both males and females (section S3). The teeth of all individuals were complete and heavily worn, which suggests that most individuals were older adults but this estimate should be taken with some precaution as the diet that was presumably composed of a substantial proportion of shellfish (as well as seasonally available seeds) would have included a high concentration of sand and grit. No instances of osteoarthritis or nutritional deficits were noted, but because of the calcium carbonate deposition and precipitation across the skeletal samples, it was very difficult to observe the presence of any pathology. Similarly, other than trace amounts of red ocher near the burial at SM4 and the complete shell of a bulimulid land snail placed with the burial at SM1, we observed no clear evidence of associated offerings. Nevertheless, the mere presence of formal burials strongly signals that these open-air sites were ritually and symbolically meaningful places.

Shells, faunal remains, and burnt clay

The three most abundant types of archaeological materials in all sites were shells, animal bones, and burnt earth (Fig. 2). Bones recovered from all strata were poorly preserved and comparable to other Neotropical faunal assemblages (*23*). Mostly for reasons of conservation and taphonomy, the fauna in the upper layers is richer than that in the lower levels (table S1). For instance, the upper layers contained abundant remains from caimans and other herpetofauna including large (boa-sized) snakes, turtles, and tegus (fig. S1). The lower layers included some identifiable bones of deer, carnivores, armadillos,

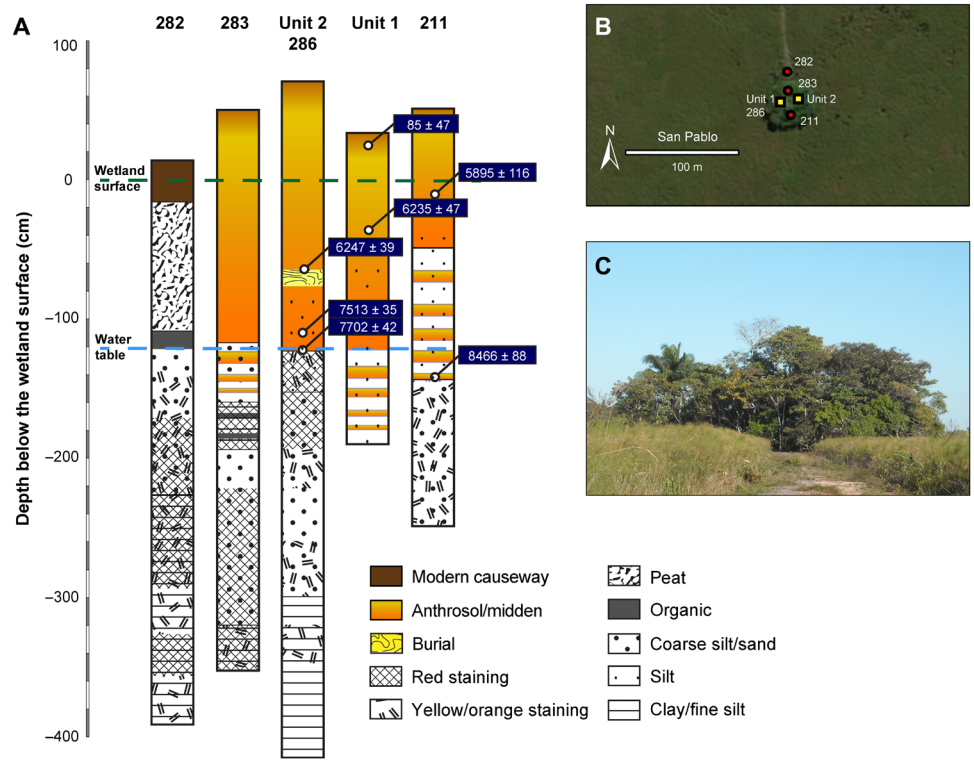

Fig. 3. Stratigraphy of cores and excavations carried out at SM4. SM4 is placed above fluvial sands that overlay clay deposits (**A**). Both the sand and clay show high levels of hydromorphism: red and yellow staining due to the formation of iron oxides. These hydromorphic conditions are typical of tropical soils subjected to repeated cycles of humid and dry conditions, as it happens in regions with strong seasonality. However, currently, these sediments are found below a wetland (**B**), suggesting that these iron oxides are a relict feature of the past, when the average water table was meters below its current depth. A view from the north (**C**) shows how today the forest island is surrounded by tall marsh vegetation and connected to the mainland by a modern causeway. Photo credits: (B) Source image: DigitalGlobe, Google Earth, and (C) José M. Capriles, PSU.

rodents, and a few birds. Some of the identified deer taxa include large and medium individuals probably representing both the marsh deer (*Blastocerus dichotomus*) and brocket deer (*Mazama* spp.). Fish remains (many of which were burned) were also ubiquitous, particularly cranial bones of swamp eels, lungfishes, and catfishes, which are typically distributed on interfluvial wetlands and archaeological sites in southern Amazonia (*24*).

The three studied sites contained shell remains in different densities (fig. S2). Whereas SM1 and SM3 contained very high densities of discarded shells, SM4 had substantially less. Mostly fragmented and therefore difficult to quantify, the shells ranged in size between 1 and 8 cm, but fragments of larger specimens were also occasionally present, suggesting the consumption of various species and sizes. Although predominant taxa were apple snails of the *Pomacea* genus (Ampullariidae), other terrestrial gastropods were also occasionally observed, including bulimulid, planorbid, and hydrobiid land snails, as well as a few fragments of freshwater bivalves. Ethnohistoric and ethnographic evidence supports the idea that people exploited apple snails in the Llanos de Moxos. For instance, an 18th century description of the Moxos Indians mentions that snails were regularly collected and consumed, particularly at the beginning and near the end of the rainy season when seasonal wetlands became murky and muddy (*25*). Because different degrees of fragmentation occur in these assemblages, it is very difficult to assess either taxonomic or size changes over time. Nevertheless, discrete layers of substantial accumulations of well-preserved unburned and unweathered shells indicate exposed trash heaps, while occupation surfaces are composed of abundant compressed, pulverized, burned, and weathered concretions.

Burned clay is never absent from site sediments, but it occurs in greater abundance within the shell midden strata. Because clumps of burnt clay were abundant in all sites, we can use this material as a proxy of human occupation intensity and energy combustion at these sites. We found the most abundant concentration of these materials in the layers associated with a probable hearth feature in SM4. Some of these burned nodules are as hard and oxidized as ceramics, suggesting that a combination of high temperatures and/or persistent fire would have been involved in their formation, possibly in connection to sustained or recurrent occupations and soil combustion activities such as land clearing, smoking, and grilling. Although charcoal was conspicuous in all sites, we collected and processed 22 bulk flotation samples, but we could only identify a few specimens of carbonized seeds and woods from the analyzed heavy and light fractions.

Regional chronology

Our current chronology is based on 88 accelerator mass spectrometry (AMS) radiocarbon dates collected from four archaeological sites and 23 buried paleosols (Fig. 5). SM1 currently bears the earliest evidence of human presence, ca. 10,600 cal B.P., based on two dates from the base of the shell midden and increased occupation intensity between 6700 and 4000 cal B.P. The development of anthropogenic sediments at SM4 starts around 8500 years ago and persists regularly for the next three millennia. At SM3, human occupation

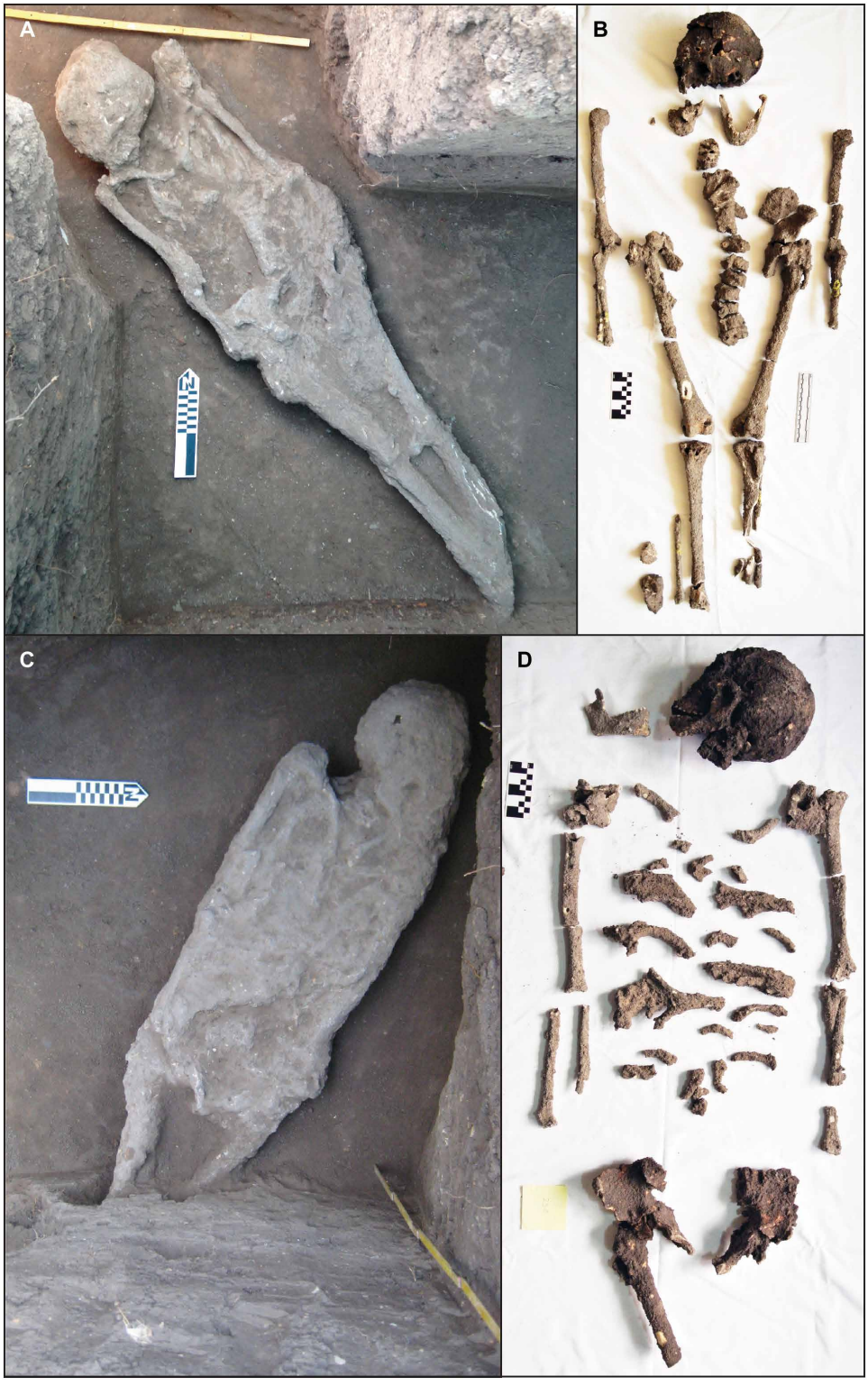

Fig. 4. Burials documented at the Llanos de Moxos site SM3 forest island. (**A** and **B**) Burial 1 and (**C** and **D**) burial 2 during excavations and after cleaning bones encrusted with carbonates. Photo credit: José M. Capriles, PSU.

and the deposition of shells and other anthropogenic sediments date as early as 8700 cal B.P. and persist until approximately 5800 years ago. This period also largely coincides with the chronology of San Francisco (SM2), another forest island containing anthropogenic sediments including shell middens, which was cored but not excavated (*19*). Overall, coinciding with the formation of various paleosols, these hunter-gatherer sites were occupied for millennia before the advent of agricultural intensification in southwestern Amazonia.

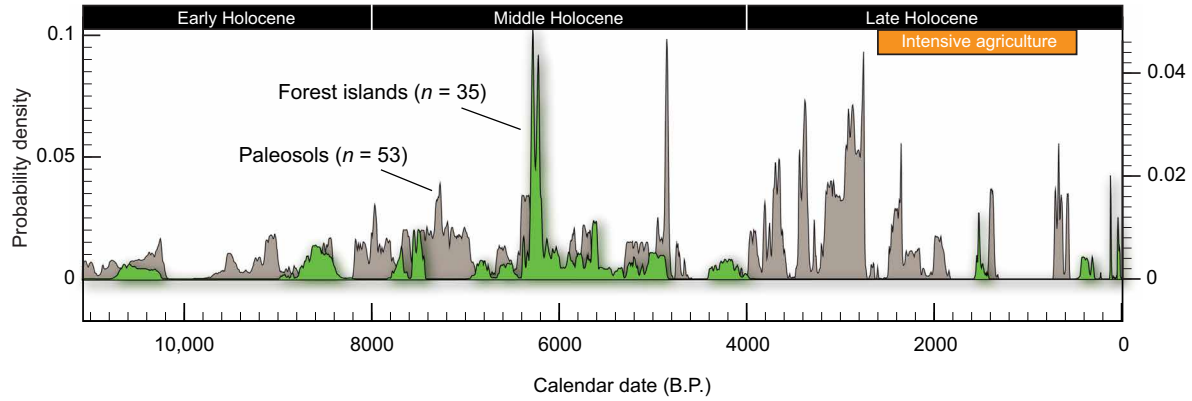

Fig. 5. Chronology of the Llanos de Moxos forest island occupations. Comparison of sum probability distribution of calibrated radiocarbon dates from the shell midden sites and regional paleosols (see table S2).

The sites we have investigated were abandoned several centuries before the Late Holocene emergence of complex agricultural societies in the Llanos de Moxos. The hiatus in the archaeological record between the tropical hunter-gatherer occupations we are describing and later agricultural societies is not necessarily an indication of regional abandonment but could be a consequence of the southern avulsion of the Rio Grande or of research bias. For instance, recent research from the shell midden or sambaquí of Monte Castelo and the riverine site of Toetônio in southwestern Brazil provides evidence for the domestication of wild rice and the existence of other cultigens during this transition (*10*, *13*). Similarly, several samples dated between 3500 and 2000 cal B.P. have been recovered from the deepest levels of some monumental mounds excavated in the central Llanos de Moxos (*26*). Some of these dates originate from "sterile" layers that predate the construction of the mounds as in the case of Loma Mendoza and Loma Salvatierra (*17*), but the existence of burned woods underneath these sites is suggestive and could indicate low-level preceramic human disturbance (*27*, *28*). Moreover, a pollen record from Lake Rogaguado, a freshwater lake located in the northwestern Llanos de Moxos, suggests increased fire activity, landscape disturbance, and potential adoption of cultigens such as maize and gourds as early as 6500 years ago (*29*). Therefore, although certain cultural and paleoecological processes hinder our understanding of the transition from tropical foragers to complex agricultural societies, potentially more sites with longer time sequences and more direct evidence of anthropogenic environmental disturbance will be eventually found as suggested by previous research in the region. For instance, charcoal deposition that predates ceramic occupations has been reported in Estancita and San Juan (7500 to 6400 cal B.P.) in the northwest Llanos de Moxos (*18*) and Granja del Padre and Bella Vista 3 (7200 to 4500 cal B.P.) in the eastern Llanos de Moxos (*30*). While these dates and their contexts suggest an ephemeral signal of the preagricultural tropical hunter-gatherers, the evidence from the Llanos de Moxos forest islands demonstrates the persistence and archaeological visibility of long-term tropical foraging in southwestern Amazonia.

DISCUSSION

The unprecedented findings reported here suggest that tropical foragers thrived and eventually generated enough environmental impact to leave tangible evidence of their presence on the southwestern Amazonian landscape much earlier than previously documented or assumed (*17*). The stratigraphic and contextual associations documented in the archaeological excavations verify the existence of anthropogenic midden layers containing abundant burnt earth, charcoal, shell, and faunal remains and therefore demonstrate that these sites were occupation loci where substantial food processing, consumption, and discard took place. The consistent finding of remarkably preserved human remains also supports that these sites were prominent foci of social and ritual activities between 10,600 and 4000 years ago. The finding of human burials is in itself a powerful indicator of reduced mobility and territoriality, as burials can provide a tangible form of legitimizing exclusive access or property rights over resource patches (*31*, *32*). Therefore, it is possible to hypothesize that the Llanos de Moxos forest islands were among the first earthworks of economic and symbolic importance built in southwestern Amazonia.

The increasingly disturbed landscape in which the Llanos de Moxos preceramic sites were formed was stable, in the sense that neither sediment deposition nor erosion took place, allowing for soil formation between the Early and Middle Holocene (*20*, *21*). Furthermore, the modern landscape bears no relation to the ancient one, which surrounded the study sites before the Late Holocene. Phytoliths and carbon stable isotope analyses suggest that, during the Middle Holocene, the central Llanos de Moxos was mostly covered by forest and cerrado-like vegetation (*33*). The occupation trajectory of these sites largely coincides with a macroregional episode of aridity during the Middle Holocene, roughly between 8000 and 5500 cal B.P., which has been linked to a weakening of the South American summer monsoon (*34*). The increased regional aridity had substantial consequences for human populations in other biomes such as the Andean highlands and the Atacama Desert, causing major population displacements and interrupting long-term trajectories of human adaptation (*35*, *36*). Nevertheless, the decrease in precipitation in most of tropical South America seems to have had a weaker effect on the human demography of the Llanos de Moxos as demonstrated by the persistence of human occupations in the region. Furthermore, vegetation reconstructions derived from pollen analyses of lacustrine sediments further verify that the decreased precipitation produced significant impacts in the Llanos de Moxos land cover involving the expansion of forests and cerrado-like vegetation (*37*, *38*). Under these dryer circumstances, productive wetlands were likely seasonal, patchy, dispersed, and potentially subject to territorial control.

The evidence manifested in our study sites suggests that tropical hunter-gatherers inhabiting the markedly seasonal landscape of the Llanos de Moxos emphasized a central place foraging strategy at least during part of the year. The inferred foraging pattern might be analogous to that practiced by the ethnographically documented Sirionó of the eastern Llanos de Moxos, who, as late as the 1940s, still relied on seasonally constrained mobility (*39*). Although the Sirionó often moved to avoid contact with white landowners, their foraging and mobility strategies largely responded to seasonal availability and accessibility of subsistence resources. Specifically, during the dry season, bands of Sirionó frequently moved between rainforest patches as they followed troops of monkeys, peccaries, and other high-return prey, while during the wet season, as rivers overflowed and pampas and forests flooded, they established more permanent residential camps above forest islands to which they tethered shorter foraging trips. Because of the reduced availability and profitability of resources, the Sirionó often practiced very simple forms of cassava and maize horticulture during the wet season.

Similarly, the structure and composition of the studied sites are consistent with residential camps tied to wetland patches and suitable locations for exploiting interfluvial aquatic resources. The abundance of *Pomacea* shells suggests two things in terms of paleoenvironments and subsistence. First, it suggests that the sites were occupied during either the beginning of the wet season or the end of the dry season, as these are the periods when they become more active and available. Second, it implies that the sites were occupied near wetlands and, more specifically, interfluvial systems. Gastropods (similar to many wild plants) are low-return food items, and their increased consumption signals an increase in the dietary breadth. Bulk collection and central place transportation of shellfish and other food resources could have maximized their return rates, as would have the increased depletion of more profitable resources. Progressive intensification could have led not only to the adoption of exogenous domesticated cultigens but also to a "familiarization" and eventual domestication of local species (*16*). The disturbance produced by these activities also generated a series of environmental transformations that, either intentionally or unintentionally, could have modified and enhanced the predictability, diversity, and density of their surrounding resources (*40*–*42*). The ritual burials found in these sites further suggest that these processes occurred in a context that favored intragroup cooperation, intergroup competition, and territoriality (*43*, *44*). The inferred recurrent site reoccupation, redundant resource utilization, food procurement intensification, reduced mobility, and increased territoriality would have provided concrete incentives for landscape investment and institutional innovation.

MATERIALS AND METHODS

We conducted systematic excavations and sediment coring in three forest island sites: SM1, SM3, and SM4. These sites are located in the central Llanos de Moxos, the area with the highest concentration of monumental mounds (*7*). During fieldwork, each forest island was cleared of understory vegetation, mapped, and test-excavated. The preservation of archaeological materials in general is very poor, as the environmental conditions have negatively affected every kind of organic material. Excavations involved handheld tools, and all sediment was screened through 6.35-mm screens. Ten-liter bulk soil flotation samples were also collected, processed, and sorted. Features such as hearths, occupation surfaces, and human burials were carefully exposed, mapped, and photographed before removal in the field. We also collected additional sedimentary cores from various portions of the forest islands using a Wacker Neuson motor vibracorer.

The recovered remains were cleaned, sorted, and tallied in the laboratory according to different material categories. Bones and shells were identified to the highest possible taxonomic and anatomic level, counted and weighed, and inspected for visible cultural and noncultural modifications. Most bones, especially from the lower levels were covered by carbonates, strongly silicified, and heavily fragmented, making them very difficult to recover, clean, and identify. Therefore, although we recorded the number of identified specimens (NISP) counts of all the identified taxa, considering the taphonomic limitations of this assemblage, our data are probably most accurate as ordinal scale, meaning that the specific NISP should only be used to estimate relative abundance and rank order of subsistence resources (*45*).

Because many layers within these sites contained abundant shell remains, dissolved calcium carbonate became encrusted directly on the surface of most skeletal elements. This resulted in a calcite covering that was difficult to remove, and mechanical methods resulted in the destruction of the outer layers of bones. To this end, we opted for removing portions of the articulated bones as whole blocks that we subsequently cleaned in the laboratory. To remove the external surface of the calcifications, some elements were processed in a 5% acetic acid solution in two treatments of 4 to 6 hours or until carbon dioxide (the result of the acid base reaction) stopped being produced. Although this was insufficient to fully remove the breccia-like matrix, it did allow for a superficial analysis of some skeletal components. In the case of human burials, sex, height, and age assessments were derived using sexually dimorphic cranial (supraorbital margin, supraorbital ridge, mastoid process, nuchal crest, and mental eminence) and postcranial pelvic rim shape (subpubic angle and concavity, greater sciatic notch angle, and ischial spine orientation) characters, measurements of selected long bones, epiphyseal fusion stages, fusion of cranial sutures, and dental tooth wear (*46*–*48*).

AMS radiocarbon dates were processed using standard methods in four radiocarbon laboratories: the Poznan Radiocarbon Laboratory, the Laboratory for the Analysis of Radiocarbon with AMS at the University of Bern, the AMS Radiocarbon Laboratory at The Pennsylvania State University (PSU), and DirectAMS. All dates were calibrated, including sum probability distributions of calibrated radiocarbon dates, using the southern hemisphere calibration curve SHCAL13 (*49*) in Oxcal 4.3 (*50*). The resulting chronology (table S2) contains 20 AMS radiocarbon dates initially documented from the Llanos de Moxos shell middens (*19*), 15 new dates collected from archaeological contexts to improve the temporal resolution of the sites, and 52 AMS radiocarbon dates from buried paleosols and other sediments previously published as part of regional paleoecological research (*20*). In addition, we also included one additional paleosol date recently published from a separate study (*51*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/4/eaav5449/DC1

Section S1. The Llanos de Moxos

Section S2. Early human adaptations to wetland environments

Section S3. Bioarchaeological description of the human burials

Fig. S1. Selected faunal specimens from the shell midden excavations.

Fig. S2. Selected well-preserved apple snail *Pomacea* shells.

Table S1. Faunal remains' NISP from each of the studied sites including their common names in parentheses.
Table S2. Radiocarbon dates from the studied sites calibrated using SHCAL13 (*49*) using Oxcal 4.3 (*50*).
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