

Supplementary Materials for

Persistent Early to Middle Holocene tropical foraging in southwestern Amazonia

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Supplementary Materials

Section S1. The Llanos de Moxos

Situated between the eastern slopes of the Andes and the Brazilian Precambrian shield, the Llanos de Moxos of southwestern Amazonia, is a seasonally flooded savanna interspersed by gallery forests flanking large rivers and their tributaries as they slowly meander towards the Amazon (52-56). High temperature, persistent humidity, and seasonally constrained rainfall characterizes the regional climate. The quantity of precipitation is largely influenced by the intensity of the South American Summer Monsoon (SASM), which brings humidity from the Atlantic into the Amazon basin as the intertropical convergence zone shifts southward during the austral summer (57). Because central and southern Llanos de Moxos are very flat, during the SASM, most rivers overflow and inundate the surrounding savannas. When rainfall recedes during the dry season, the savannas progressively dry up. Decadal to centennial patterns of rainfall variation enhance or limit the spatial and temporal extent of flooding and potential changes in the hydrological system (58, 59).

Patches of forests remnants and isolated forest islands are often associated with paleo-levees that document a dynamic Quaternary hydrological system characterized by frequent fluvial avulsions and formation of crevasse splays (20, 21). While at decadal to annual time scales the alluvial plains dynamics of the Llanos de Moxos seems to be independent from climate, or at least from the ENSO cycles (59); at longer (millennial) time scales, climate has been identified as the principal driver of changes in river behavior (21). Neotectonics however, was also an important driver of landscape-scale changes in the Llanos de Moxos throughout the Quaternary (53, 60-62).

In the central and southern Llanos de Moxos, most of the savanna is established on the river-backswamps while forest grows on relatively elevated fluvial deposits, mostly fluvial levees and crevasse splays. Here, the forest-savanna ecotone is controlled by the local hydrology: as backswamps are flooded during the rainy season and then undergo severe water stress during the dry season, generating a hostile environment for trees to grow. On the contrary, as fluvial deposits are elevated over the landscape and remain above the water level for most of the year, they are covered with evergreen forest (54, 63). In the northern part of the Llanos de Moxos, forests normally grow on large outcrops of the Brazilian shield. Here it has been shown that the tree cover is relatively recent, as forest began to replace savannas as result of an increase in precipitation that started around 4,000 years ago (37, 38). In contrast, during the same time, savannas have been progressively replacing forests in most of the central and southern Llanos de Moxos (33).

Abundant archaeological and paleoecological data suggest that significant landscape-scale transformations of southwestern Amazonia began during the late Holocene (18, 30, 37, 64, 65). Most of the known large scale earthworks in the Llanos de Moxos have been radiocarbon dated to the later part of the late Holocene (2,500-500 cal BP) (17, 26, 66, 67) and were likely developed as a complex adaptive system to the recurrent pattern of seasonal flooding (68). Large mounds connected by causeways and canals are thought to have been designed to create occupation surfaces and communication networks between them (8, 52, 69). Other features, including raised fields, might have been constructed to drain excessive floodwater away from agricultural fields (51, 70). The amount and intensity of construction observed in the Llanos de Moxos during the late Holocene is remarkable, but very little is known about the origins of these cultural systems, how previous societies responded to the dramatic environmental changes the region experiences on a seasonal basis or about the behavioral context that prompted tropical hunter-gatherers to engage in agriculture (71-75).

Section S2. Early human adaptations to wetland environments

There are a number of reasons why, notwithstanding a century of archaeological research, no early human occupation had been reported until very recently in the Llanos de Moxos (17, 76). Many of the early archaeological sites in the region were buried or eroded by fluvial alluvium (20), the region lacks stone outcrops that could have helped to locate settlements or sources of raw material to manufacture stone tools, and most archaeological research has focused on later ceramic occupations. Nevertheless, archaeological and paleoecological studies are increasingly supporting a significantly complex and long-term relationship between humans and Amazonian ecosystems over much of the Holocene (5, 12, 13, 18, 29, 77-79). The earliest evidence of human foraging in the Llanos de Moxos

consists of open-air sites including shell middens deposited underneath forest islands (19), which are the focus of this research.

Shell middens are formed as a result of the deliberate collection and transport of shellfish such as gastropods and bivalves, from their aquatic habitats to specific consumption and discard loci (80). Humans have collected and consumed aquatic resources since at least the Middle Stone Age (81, 82). In the New World, shell middens are common in most coastal settings and span millennia (83-88). For instance, in the Peruvian and Chilean coasts, many well-stratified shell middens have been excavated and contain evidence of domestic, ritual, and funerary activities (36, 89-92). In the southeastern coast of Brazil, some of the largest shell middens of the continent are locally known as sambaquis (93-95), and in the lower Amazon basin, Taperinha is a shell midden that bears evidence of ceramic manufacture dating to 8,000 years ago (96). Sites of comparable antiquity have also been reported along the shores of the Guapore and Madeira rivers of southwestern Brazil (10, 13, 97, 98). The location, distribution, and contents of these sites are excellent sources of information about human foraging behavior (99, 100).

A number of different models have been developed to explain the adaptive behavior of hunter-gatherers (101-107). By emphasizing different dimensions of foraging behavior and placing specific constraints and thresholds that would favor the adoption of certain food procurement strategies over others, optimal foraging models have been successfully applied to explain the trade-offs involved in the transition from foraging wild resources to producing food (108-111). For instance, the diet breadth or encounter-contingent prey choice model predicts whether a forager would procure a prey once encountered or continue searching for a more profitable one based on its post-encounter return rate (112, 113). Similarly, the patch choice model predicts whether a forager would stay or leave a foraging patch depending on the patches' return rates adjusted for the cost of traveling between patches. Finally, the central place foraging model predicts the decision whether to consume or transport a resource from its foraging location to a central place depending on its processing costs (114-116). Low-calorie foods such as shellfish, wild rice, nutshells require more processing than hunted prey, but these costs can be offset by bulk-processing in a central place.

Hunter-gatherer open-air sites -including shell middens- formed by the accumulation of consumption and discard activities are effectively central places and as such, they can provide key insights into the behavioral, social, and environmental conditions that shaped their use and formation (103). Based on the above we expect that the structure and composition of these sites will reflect the constraints faced by foragers including the degree of resource availability, foraging pressure, and landscape modification. For instance, foraging intensification can decrease patch return rates and prompt for increased mobility, the disturbance produced around a central place can increase the predictability and density of generalist prey and plant resources (41). Over time, the formation of central places can produce a distinctive pattern of landscape modification that could buffer against depressed resource availability and reduced mobility. Nevertheless, because plant resources are generally more abundant, bulkier and have lower return rates than wild animals, adopting agriculture can result from a decrease in the availability of higher-return hunting resources as much as from increased population densities (108).

Section S3. Bioarchaeological description of the human burials

Isla del Tesoro (SM1): The first burial was identified approximately 1.3 m below the surface in Unit 3, Locus 148. The individual lay in supine position parallel to the main axis of the unit, west to east, with the head at the northwest end. The burial was surrounded by a bed of large and medium well-preserved shells near the water table at the time of the excavation. The bones were completely covered in shells, concretions, and carbonates. The cranium was fragmented, apparently facing its right side. The arms lay straight, with the wrists crossed behind the hips. The absence of some bones (including the upper portion of the right humerus) is likely the consequence of taphonomic change such as bioturbation, as there is no reason to assume the burial was incomplete due to the positioning of the arms in an anatomically accurate position. Estimation of sex and age was difficult due to the fragmentary nature of the cranium and pelvis, which were thoroughly covered by calcium carbonate incrustations. However, the morphology of the mandible was more easily accessible and based on the robusticity, size, and gonial flare, it likely corresponds to an adult male. The heavily worn dentition suggests he was approximately 45-50 years old. Stature estimation based on algorithms for European and Mexican males from the right femur suggest the individual was approximately 1.80 m in height.

San Pablo (SM4): A second burial was found in San Pablo's Unit 2 (Locus 125). The individual was found in supine position and did not contain any visible offerings. The individual was oriented west to east with the head facing north. The skeletal elements were heavily mineralized, and most bones were fragmented and difficult to reassemble. The mandible was semi-complete and suggests the individual was an adult male based on robusticity and gonial flare. Around the body lay several clumps of burned earth, carbonate calcium concretions, and some small nodules of red ocher, possibly left as part of a burial offering. The contour of the body is delimited by a slight change in the color of the clay matrix from dark black in the interior to dark gray towards the outside suggesting the burial was placed on a pit. Other than inferring an adult age based on the presence of multiple fused epiphyses, it was not possible to recover any conclusive information from this individual as the bones were completely covered in concretions. Although San Pablo is the site where fewer shells were found during excavations, the human remains were still heavily affected by mineralization processes and covered by carbonates. In addition to this burial, we recovered the partial remains of a radius and ulna from a probable second burial in Unit 1 (Locus 105).

La Chacra (SM3): Three Individuals were recovered from La Chacra. Burial 1 (Locus 234) was found in supine position with the skull tilted to the right side. The skeleton was nearly complete with most of the cranium and post-cranial elements present. The cranium and mandible were nearly complete, and the rest of the axial skeleton included several proximal cervical vertebrae, and most of the thoracic (including rib fragments) and lumbar vertebrae in various states of preservation. Partial pelvic bones on the left side included most of the ilium and ischium. For the upper limbs, the humerus, radius, and ulna from both sides were either complete or nearly complete. For the lower limbs, complete right and left femora were recovered, including the proximal half of the tibia and fibula on the left side, and the complete tibia and distal half of the fibula on the right side. Sex estimation based on cranial and pelvic features suggest the individual was likely a female. Stature estimation was calculated according to algorithms for European females, as data was not available from Central or South American female populations, from slightly extrapolated measurements (due to damage at the proximal and distal epiphyses) of left humerus, left radius and left femur lengths resulting in an average height estimate of 1.61 m in height. While the epiphyses and cranial sutures were very difficult to see because of the calcium carbonate deposits, permanent dentition was complete, and most teeth were heavily worn. Dental wear suggests an age between 45-55 years.

The second burial (Locus 250) from La Chacra was found in supine position as an undisturbed burial with the skull tilted towards its left side. The skeleton was only excavated down to the pelvis on the left side and the proximal half of the femur on the right as it protruded into the eastern profile of Unit 3. The axial skeletal components included the complete cranium, mandible, proximal cervical vertebrae, and a large number of rib fragments. Partial pelvic bones included most of the ilium and ischium on the left side, and most of the ilium, ischium, and pubis on the right. For the upper limbs, fragments of each scapula were recovered with nearly complete clavicles. On the left side, the complete humerus, radius and ulna were recovered whereas on the right side, the complete humerus was recovered with only partial aspects of the radius and ulna. The only lower limb element recovered was the proximal half of the right femur. Cranial features suggest the individual was likely a male. Stature estimation based on algorithms for European and Mexican males from slightly extrapolated measurements of the left humerus and left radius lengths (due to slight damage at the proximal and distal epiphyses) suggest the individual was approximately 1.72 m in height. While the epiphyses and cranial sutures were very difficult to see because of the calcium carbonate deposits, permanent dentition was complete, and most teeth were heavily worn. Dental wear suggests an age between 45-55 years, and perhaps slightly older.

The third burial from La Chacra (Locus 235) was found near the end of excavation of Unit 2 as the excavation reached the water table. The position of the burial is uncertain as most elements, including the cranium were comingled possibly as a consequence of post-depositional disturbance. The finding of the articulated right femur and tibia suggest this individual might have been placed in flexed position. The axial skeletal components include the complete cranium and mandible, with cervical vertebrae 1-6/7 still attached. Fragmented ilium and ischium elements were recovered for both sides of the pelvis. The right upper limb included a partial scapula, with most of the humerus, radius, and ulna heavily fragmented. On the left, the scapula and nearly complete humerus were present. For the lower limbs, nearly complete femora, tibiae, and fibulae were recovered on the right and left sides. A large number of other small fragments including hand and foot bones were also recovered. Sex estimation based on the cranium suggests the individual was likely a male. Height estimation based on measurements of femur and tibia suggest an approximate height of 1.79 m. While the epiphyses and cranial sutures were very difficult to fully read under the calcium carbonate deposits, the teeth were heavily worn and suggest an age estimation of 45-55 years.

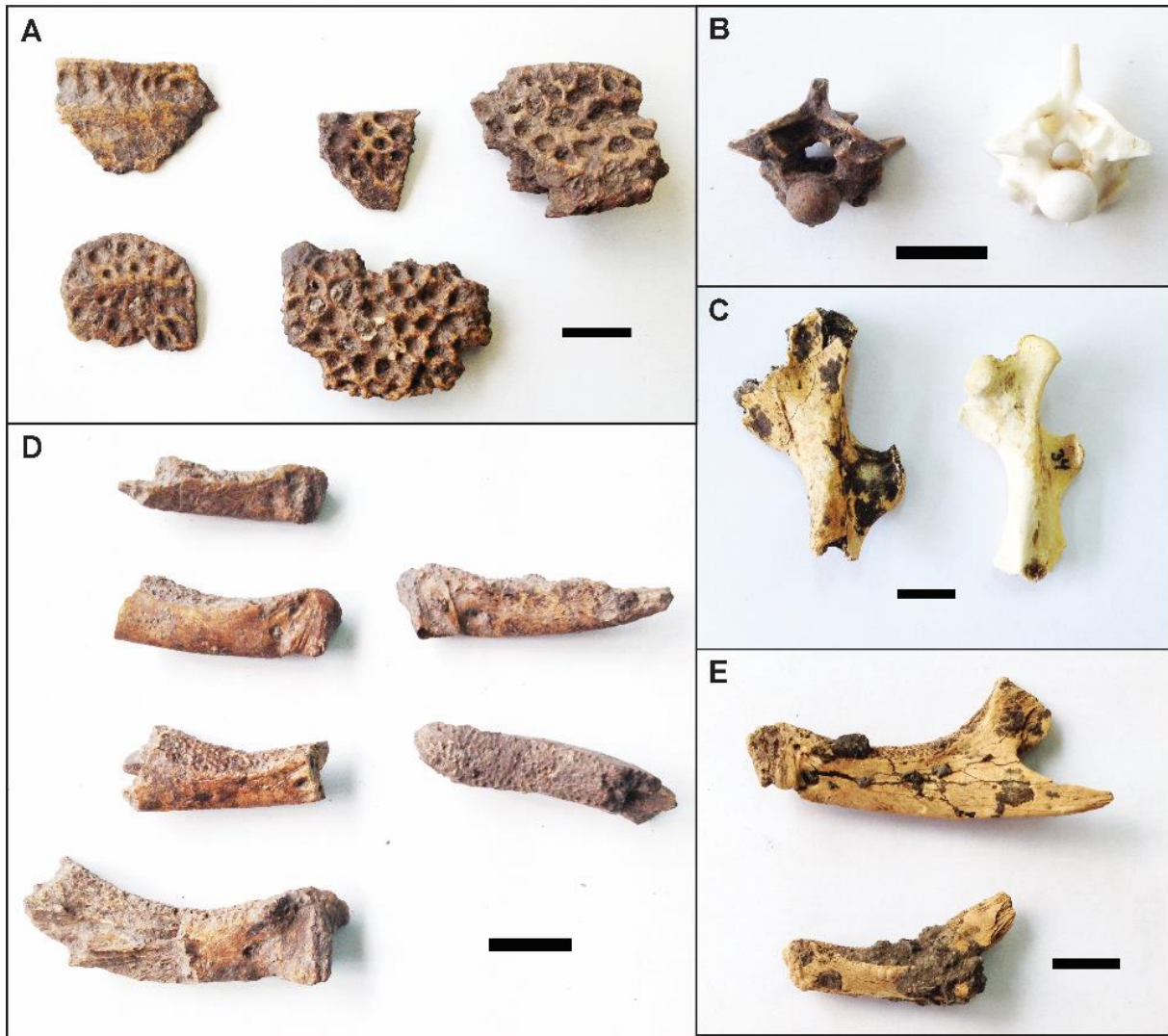


Fig. S1. Selected faunal specimens from the shell midden excavations. Bone remains include (A) caiman cranial bones, (B) large snake vertebra compared to a modern *Boa constrictor* reference specimen, (C) armadillo proximal humerus compared to a modern *Dasypus* reference specimen, and (D, E) Synbranchidae eel dentaries. Scale bars correspond to 10 mm. Photo Credits: José Capriles, PSU.

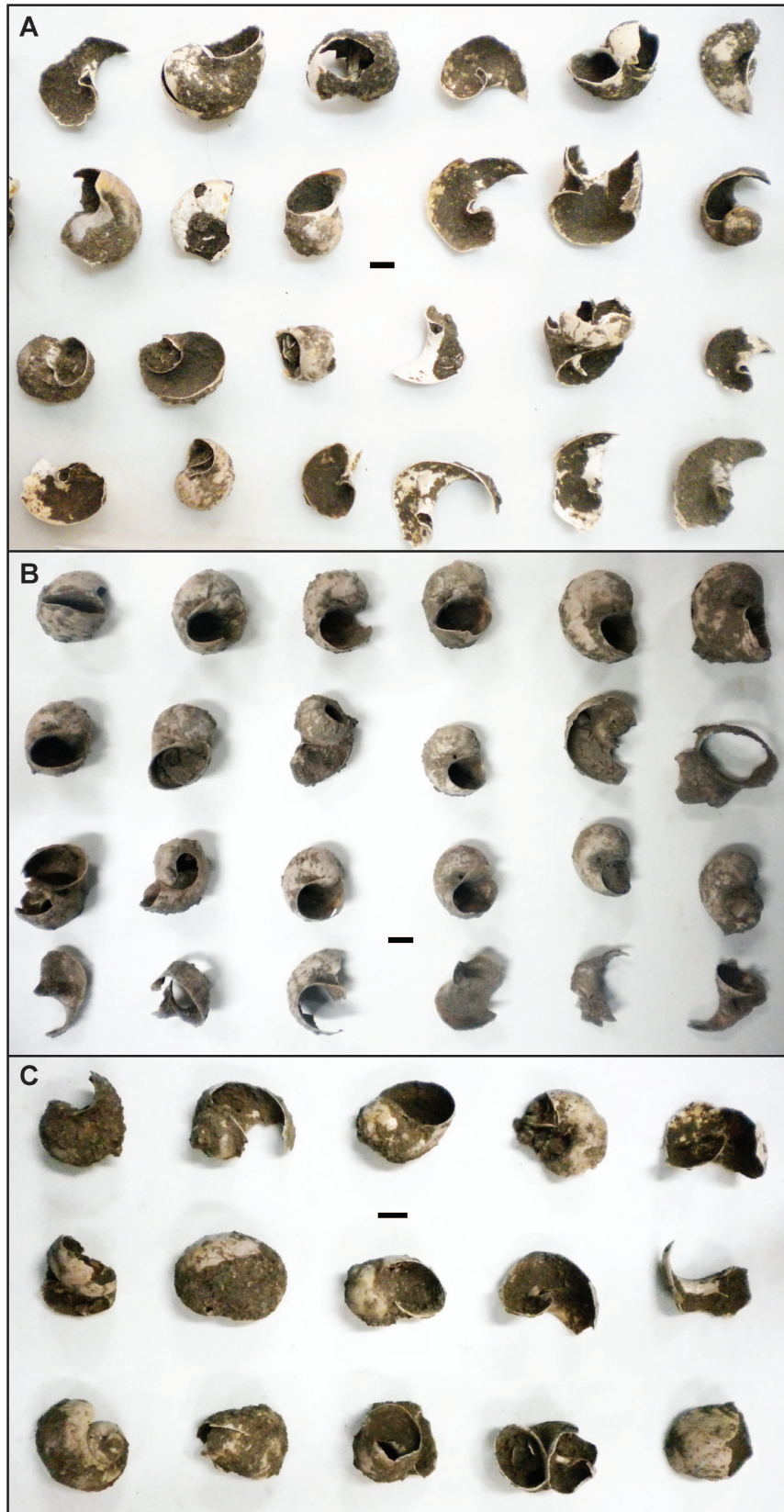


Fig. S2. Selected well-preserved apple snail *Pomacea* shells. Panels show shells from three different contexts exhibiting different preservation and weathering conditions: (A) Locus 202, (B) Locus 210, and (C) Locus 203 from the site La Chacra. Scale bars correspond to 10 mm. Photo Credits: José Capriles, PSU.

Table S1. Faunal remains' NISP from each of the studied sites including their common names in parentheses.

Identified taxa	SM1	SM3	SM4	Total
Mammalia				
Artiodactyla	1060	14	1092	2166
Cervidae (Deer)	9	11		20
Carnivora	11	2		13
Dasypodidae (Armadillos)	4	5	4	13
Rodentia	2		1	3
Large mammal	11	1		12
Medium mammal		10		10
Small mammal	5	3		8
Indeterminate	13	57	18	88
Human (commingled)	162	4	3	169
Aves				
Large bird	3	3		6
Mid-sized bird	1	17	1	19
Reptilia				
Caimaninae (Caimans)	240	20	15	275
Testudines (Turtles)	1	1		2
Teiidae (Tegus)	1			1
Serpentes (Large snakes)	2	14		16
Indeterminate		7		7
Amphibia				
Anura (Large frogs)		1		1
Osteichthyes				
Lepidosirenidae (Lungfishes)	4	1		5
Symbrachidae (Swamp eels)	18	8	3	29
Siluriformes (Catfishes)	7			7
Indeterminate	310	8	146	464
Mollusca				
Bivalvia		3	1	4
Hydrobiidae		1	1	2
Planorbidae	1		38	39
Bulimulidae	1	1	1	3
Ampullariidae	46177	2512	8116	56805
<i>Pomacea</i> large	5	11	13	29
<i>Pomacea</i> medium	93	1038	190	1321
<i>Pomacea</i> small	90	254	18	362
Shell concretions	54	11		65
Total	48285	4018	9661	61964

Table S2. Radiocarbon dates from the studied sites calibrated using SHCAL13 (49) using Oxcal 4.3 (50).