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Early Holocene crop cultivation and landscape modification in SW Amazonia

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Abstract

The beginning of plant cultivation is one of the most important cultural transitions in human history[1–4]. Based on molecular markers showing the genetic similarities between domesticated plants and wild relatives, south-western Amazonia has been proposed as one of the early centres of plant domestication[4–6]. However, the nature of the early human occupation and the history of plant cultivation in south-western Amazonia are still little understood. Here, we document the cultivation of *Cucurbita* at ca. 10,250 cal yr BP, *Manihot* at ca. 10,350 cal yr BP and *Zea mays* at ca. 6,850 cal yr BP in the Llanos de Moxos. We show that, starting ca. 10,850 cal yr BP, pre-Columbians created an anthropic landscape made of approximately 4,700 artificial forest islands within a treeless seasonally flooded savannah. Our results confirm the Llanos de Moxos as a hotspot for early plant cultivation and demonstrate that ever since their arrival, humans have caused a profound alteration of Amazonian landscapes, with lasting repercussions for habitat heterogeneity and species conservation.

Recent genetic and archaeological evidence suggests the existence of at least four independent centres of early Holocene domestication, two in the Old World and two in the New World (Mesoamerica and northern South America)[1]. However, the closest wild ancestors of several globally important domesticated cultigens occur in south-western (SW)

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Competing interests: The authors declare that they have no competing interests.

Data and materials availability: All data needed to evaluate the conclusions in the paper are included in the paper or in the Extended Data. Code used for 14C calibration in OxCal is available in Supplementary Information.

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Amazonia. These include the wild ancestors of manioc (*Manihot esculenta*) *M. e.* subsp. *flabellifolia*[7]; squash (*Cucurbita maxima* spp*. maxima*) *C. m.* spp. *andreana*[8]; peach palm (*Bactris gasipaes*)[9]; jack bean (*Canavalia plagiosperma*) *C. piperi*[4] and chili peppers' (*Capsicum baccatum* var. *pendulum*) *C. baccatum* var. *baccatum*[10]. This suggests that SW Amazonia could be the fifth global early Holocene centre of domestication. However, with the exception of *Calathea* sp. phytoliths, possibly representing lerén (*C. alluoia*), recently documented in the upper Madeira[11], archaeological evidence has not been found for early plant cultivation in SW Amazonia. Our research fills this gap with new data from 61 early and mid-Holocene archaeological sites that we refer to as forest islands (FIs)[12–14] because they now occur as patches of forest surrounded by savannah.

Mapping of forest islands

Using remote sensing data, we mapped 6643 FIs in the Llanos de Moxos (LM). The average size of FIs is 0.5 ha (min: 0.05 ha; max: 16 ha; SD 0.65 ha). We surveyed 82 of these, which represents ca. 1.2% of all sites. We took column sediment samples in all of them and carried out archaeological excavations in four. Out of the total 82 sites sampled, 83 including Monte Castelo in Brazil[14], we classified 64 sites as anthropic, based on the presence of deep dark sediments rich in organic matter, charcoal, and burned earth frequently associated with shell and bone fragments (Fig. 1). The FIs surveyed are between ~0.5 m and 3 m high. The proportion of anthropic vs. natural sites suggests the existence of at least 4700 anthropic FIs in the LM (Fig. ED1). This is probably far less than the original amount built in the early and mid-Holocene, as during the transition to the late Holocene, most of the rivers in the SW part of the LM became very active and many of the pre-existing soils and potential archaeological sites were covered by alluvial deposits, sometimes up to 5 m thick[15]. This explains the modern distribution of FIs and why 48% of the 6643 FIs we mapped are concentrated in a relatively small area in the north-western LM (Fig. ED1), where the landscape did not change notably during this period. Anthropic FIs are mostly located in interfluvial settings covered by seasonally flooded savannahs, and they account for an estimated 24 km^2 of forested area and 1,000 km of forest/savannah ecotone.

Sixty-six AMS ^{14}C dates from 31 archaeological sites (Table S1) bracket the human occupation of FIs throughout the Holocene between *ca.*10,850 and 2,300 cal yr BP. Except for three sites in the north-eastern LM dated at *ca*. 2,350, 2,350 and 4,100 cal yr BP, the remaining dated sites were established between the early and mid-Holocene.

Evidence of early plant cultivation

We analysed phytoliths from the radiocarbon-dated profiles of 30 FIs (Figs. 2, 3). The earliest evidence of *Manihot* is a heart-shaped phytolith[16] documented at the Isla Manechi dated *ca*. 10,350 cal yr BP and in Isla del Tesoro dated *ca*. 8,250 cal yr BP (Fig. 1). Scalloped sphere phytoliths derived from the rind of *Cucurbita* sp. were identified in layers dated to *ca*. 10,250 cal yr BP in Isla Manechi and *ca*. 9,850 cal yr BP in Site 575. We have identified wavy-top rondel phytoliths, produced in the cob of maize[17], dated *ca*. 6,850 cal yr BP (Site 570) and *ca*. 6,700 cal yr BP (Site 421). We detected the early presence of Marantaceae *Calathea* sp. rhizome phytoliths at *ca*. 8,275 cal yr BP (Isla del Tesoro), before *ca*. 7,800 cal yr BP (Site 433) and at *ca*. 7,400 cal yr BP (Site FIN 14). Other Marantaceae, Cyperaceae, *Phenakospermum guianensis*, and *Heliconia* phytoliths have been found in almost all the samples starting from *ca*. 10,400 cal yr BP (Fig. 2, S2). We identified *Oryza* seed phytoliths dated at *ca*. 6,250 cal yr BP (San Pablo); and phytoliths from the epidermis of *Celtis* seeds from contexts dated to *ca*. 9,600 cal yr BP (Site FIN8). Hat-shaped and globular echinate phytoliths diagnostic of subfamily Arecoideae[17] of the palm family (Arecaceae) are present at *ca*. 9,975 cal yr BP (site 493). Peach palm (*Bactris* sp.), a member of this subfamily, is the only palm domesticated in South America, and its domestication likely took place in SW Amazonia[6]. *Bactris* produces these hat-shaped phytoliths, but does not produce diagnostic phytoliths at the species level[18]. *Bactris* and other arecoid genera growing today in the LM (*Astrocaryum*, *Desmoncus*, *Geonoma* and *Socratea*), are used for food, building materials and medicine in present Amazonia[19]. The size of squash phytoliths is well in the range of the domesticated species (table ED2), however, they do not show increase in size over time as would be expected under domestication pressure (Table. ED2)[17].The presence of domesticated *Cucurbita* sp. beginning at ~10,250 cal yr BP in Isla Manechi is the oldest evidence of *Cucurbita* sp. in Amazonia and coincides with the domestication of several species of *Cucurbita* across Central [20] and South America[21,22] at the very beginning of the Holocene. Further studies analysing larger sample sizes are needed to determine whether the domesticated squash cultivated in the early Holocene was adopted in the LM from other regions or was domesticated *in situ*. Maize cob phytoliths were documented at site 570 ca. 6,850 cal yr BP representing the oldest evidence, by a few centuries, of maize cultivation in the Amazon basin. As hypothesized by Kistler et al.[23], early maize in this and other areas probably represented a partially domesticated variety that later diverged into two South American groups of fully domesticated maize varieties. This early evidence of maize phytoliths is consistent with a temporal gradient of maize dispersal that began in western Amazonia and reached the eastern Amazon by ~4,300 cal yr BP. The early use of *Manihot* in Isla Manechi in the LM began more than 10,000 years ago, which coincides with the time of estimated molecular divergence from the wild ancestor and with current biogeography of manioc's closest wild ancestor[7,24]. It possibly spread later to northern Peru (8,500 cal yr BP), Colombia (7,000 cal yr BP) and Panama (7,600 cal yr BP)[5]suggesting the bi-directional exchange of cultivars between Amazonia and the Andes beginning since the early Holocene. Our study shows that, as in other regions of Amazonia and Central America, also in the LM the development or arrival of full-blown agricultural societies was a very late phenomenon[9], as there is no evidence of land prepared for agriculture in the LM until raised fields and drainage canals were built around 1,500-1,000 years ago[25].

The importance of starch-based foods

Paleoecological studies indicate that the LM was covered by cerrado-like savannah during the early and mid-Holocene[15] indicating that plant cultivation in the Neotropics also started in shrub savannahs along with seasonal tropical forest environments[4]. It does not come as a surprise that phytoliths derived from plants producing underground storage organs constitute an important part of the total phytolith assemblages from the LM's FIs including *Manihot*, *Calathea* and other Marantaceae, *Heliconia*, Cyperaceae and *Phenakospermum*. These

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plants, which are abundant in savannahs, produce carbohydrate-rich foods which, with the exception of some varieties of manioc[27], are easy to process and cook. They are nowadays consumed by indigenous groups[19] and probably provided a considerable part of the calories consumed by the first inhabitants of the LM. Large herbivores and fish available in the savannahs[12,13] would have complemented a mixed economy. The fertile FIs were probably the home gardens where these crops were cultivated. Our data are in agreement with the hypothesis that plants producing underground storage organs were a fundamental part of the diet of human populations colonizing new territories[28,29].

Implication for biodiversity

Our results show that inland savannahs were a key region for the early occupation of Neotropics and that they began to be transformed by the arrival of very early human settlers. FIs are entirely anthropic. However, their formation is not only an incidental effect of food-waste dumping, but it can also be seen as an active process of niche construction[30]. These accumulative middens also constitute fertility hotspots amid poor savannah soils, since: i) they became *loci* for the accumulation of nutrients that come from gathering activities in the surrounding savannah, and ii) they remained above the water level during the wet season[12]. It is only after 4,000 years BP, when the old and infertile soils of the south of the LM were covered with fertile alluvium deposited by the Río Grande, that agriculture in the savannahs was facilitated[31]. Overall, the construction of pre-Columbian FIs, which became key structures in the landscape[32,33], increased forest patchiness (Fig. ED3, ED4a) and probably contributed to maintaining landscape-scale species richness in this Ramsar threatened biome. Nowadays, these anthropic FIs are preferential feeding and roosting sites for many species of birds, including the endemic and critically endangered blue-throated macaw (*Ara glaucogularis*)[34]. Taken together, our data show that the earliest inhabitants of the LM were not just tropical hunter-gatherers, but colonizers who had engaged in plant cultivation since the early Holocene, thus opening up the possibility that they already had a mixed economy when they arrived in the region. The thousands of keystone structures represented by FIs show that the human footprint on Amazonia is not just restricted to large-scale transformations by late Holocene farming groups[9,35], but is rooted in the earliest human dispersal into this region and has lasting implications for habitat heterogeneity and biodiversity conservation.

Methods

Mapping of FIs

FIs were mapped by visual scanning of high-resolution satellite imagery of Esri ArcGIS basemaps (Fig. ED5). When the identification of FIs was not straightforward due to cloud cover or poor resolution, TanDemX and SRTM digital elevation models were used as complementary resources. Patches of forest were classified as FIs when they had a round shape and were completely or partially surrounded by savannah (n = 4,341); or they had an irregular shape but were relatively small (<400 m in diameter) and completely surrounded by savannah (n = 2,304). For each FI, the following attributes were recorded: diameter; shape (perfectly round, almost round, elongated or irregular); location (along paleochannel,

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along modern river, seasonally flooded savannah, border between seasonally flooded savannah and upland, along a drainage stream, upland surrounded by bushes); presence of other earthworks within ~500 meters; and whether or not FIs were established over fluvial deposits or uplands. The latter attribute is partly redundant with “Location” but sometimes fluvial deposits are not connected to paleochannels (as in the case of old crevasse splays or old meander belts where paleochannels have been infilled) or the FIs are located along a paleochannel with completely eroded levees and the FIs have clearly been built after the erosion of the levees.

Selection of survey areas

Four survey areas were selected in different regions of the LM to ground-truth FIs and evaluate their natural or anthropic origin. The four areas (Fig. 1) were selected based on differences in soil, landcover, hydrology, and accessibility by car. These four areas cover all the different eco-regions identified in the LM[36,37]. These areas belonged to organizations (area a -see inset in Fig. 1- in the Barba Azul Nature Reserve) or ranchers (b, c, and d) who granted us permission to conduct surveys. In total, we surveyed 21 FIs in area a, 22 in b, 13 in d, and 17 in e. Nine other FIs were surveyed outside of these four areas.

Criteria for identification of anthropic FIs

Several anthropic FIs in the LM have been excavated [12–14]. These excavations have revealed thick strata of sediments rich in organic matter, charcoal, burnt earth, and fragmented animal bones and shells; they also have revealed human burials. The clear difference between the sediments found in the anthropic FIs and the soil types found in the LM[38–41] makes the field identification of FIs relatively straightforward. In the present work, the FIs surveyed have been classified as anthropic when thick layers of organic-rich sediments contained at least two archaeological materials such as charcoal, burnt earth, animal bones, and shells.

Sampling of FIs

Sampling of undisturbed material was performed at regular intervals in the four sites where archaeological excavations were conducted: Isla del Tesoro (SM1), La Chacra (SM3), San Pablo (SM4), and Isla Manechi (Fig. ED6). The rest of the sites were sampled using an auger soil sampler. The stratigraphy of the recovered cores was described in the field and sampling was carried out only where stratigraphic changes were detected in the field (Fig. ED7). The deepest sample with evidence of charcoal was always sampled. After extraction, cores were inspected to avoid contamination and check that the soil section sampled show no evidence of soil mixing (i.e. root penetration and invertebrate burrowing were absent). The excess of material has been cut off with a knife and only the inner, uncontaminated part of the extracted samples has been stored in plastic bags. Samples have been air-dried in Bolivia before being shipped. Charcoal fragments for 14C have been collected in situ, enveloped in aluminium foil and stored in plastic bags.

Phytolith processing and identification

Phytoliths were extracted from sediments following Lombardo et al.[42]. Phytoliths were identified and counted using a Zeiss Axioscope 40 light microscope at 500× magnification.

Phytolith identifications were made using published material for the Neotropics[17,43–46] and by direct comparison with the phytolith reference collection of the Archaeobotany and Palaeoecology Laboratory in the Department of Archaeology of the University of Exeter. A minimum of 200 diagnostic phytoliths were counted per slide. A full scan of the slides was performed to detect the presence of squash, manioc and maize. Phytolith assemblages in SW Amazonia have been studied in modern soils[46] and 29 paleosols from the early and late Holocene[15] in different natural environments and land covers. In none of these natural contexts have phytoliths of Manihot or Curcubita been found, strongly suggesting that phytoliths of these two genera found in FIs are the direct result of human activity and not of the chance occurrence of wild relatives on these FIs

Radiocarbon dates

The deepest recoverable sample of charcoal from 32 sites was dated in order to establish the minimum age of site foundation. For the four sites that were excavated, 35 samples from different depths were dated in order to establish periods of occupation and abandonment. The complete dataset and code used to calibrate all of radiocarbon dates are available respectively in Table ED1 and Supplementary Information. Radiocarbon dates from the studied sites were calibrated using SHCAL13[47]. For Isla del Tesoro, Isla Manechi and La Chacra, where stratigraphically ordered ages were available, we run a series of Bayesian age-depth models using the P_Sequence command in OxCal 4.3[48] with default settings. Each model was stratigraphically constrained by the youngest age in the profile and the deepest section reached in each site (Fig. ED8). Ages of undated samples were estimated using the command Date within the model.

Extended Data

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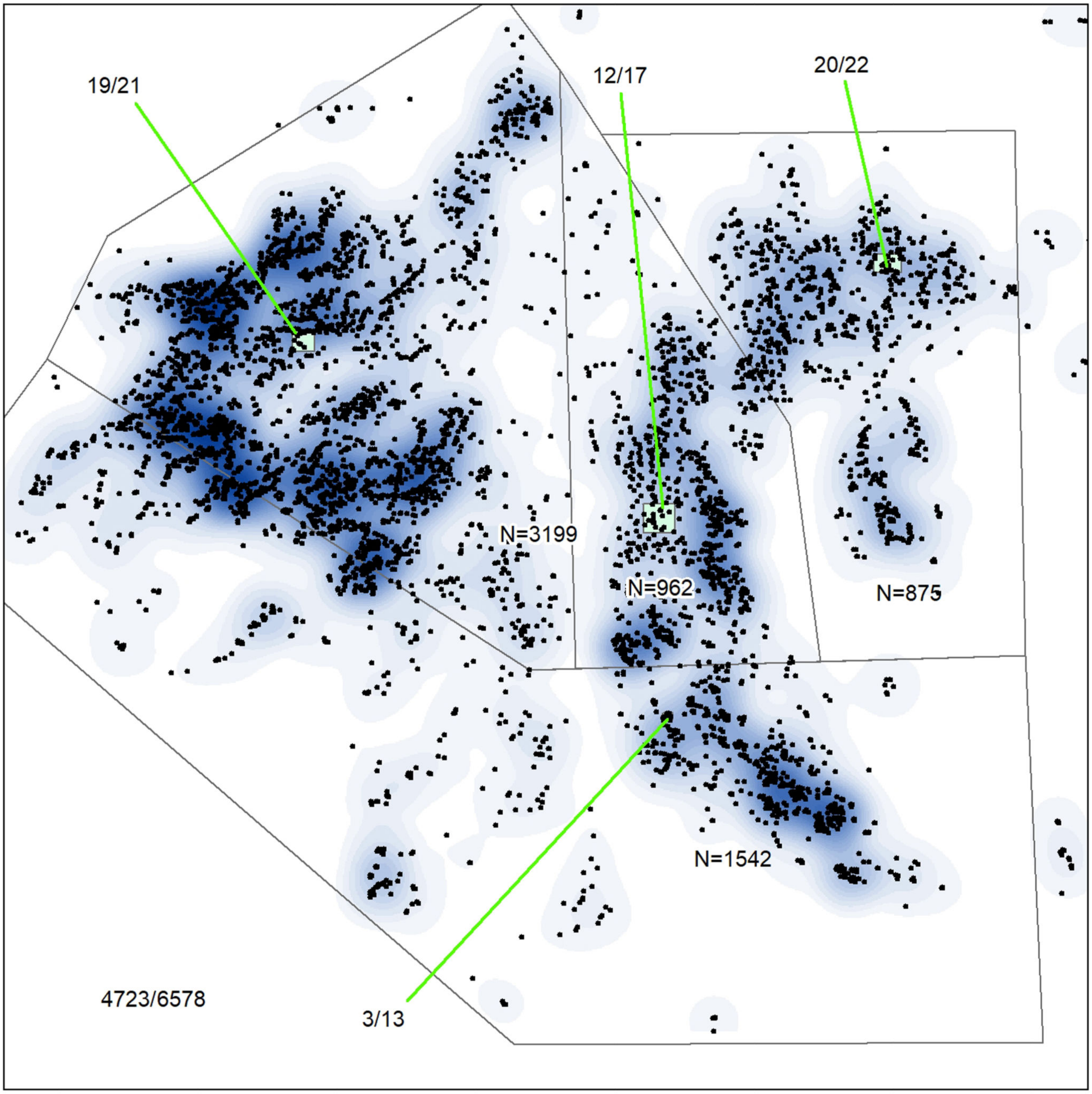

Fig. ED1.

Estimated number of anthropic FIs. The number was estimated by extending the proportion of anthropic FIs in the surveyed areas (in green) to the portion of the LM with similar physical geography and land cover (polygons). Background image represents the density of FIs, calculated using the Kernel Density tool in Esri ArcGIS.

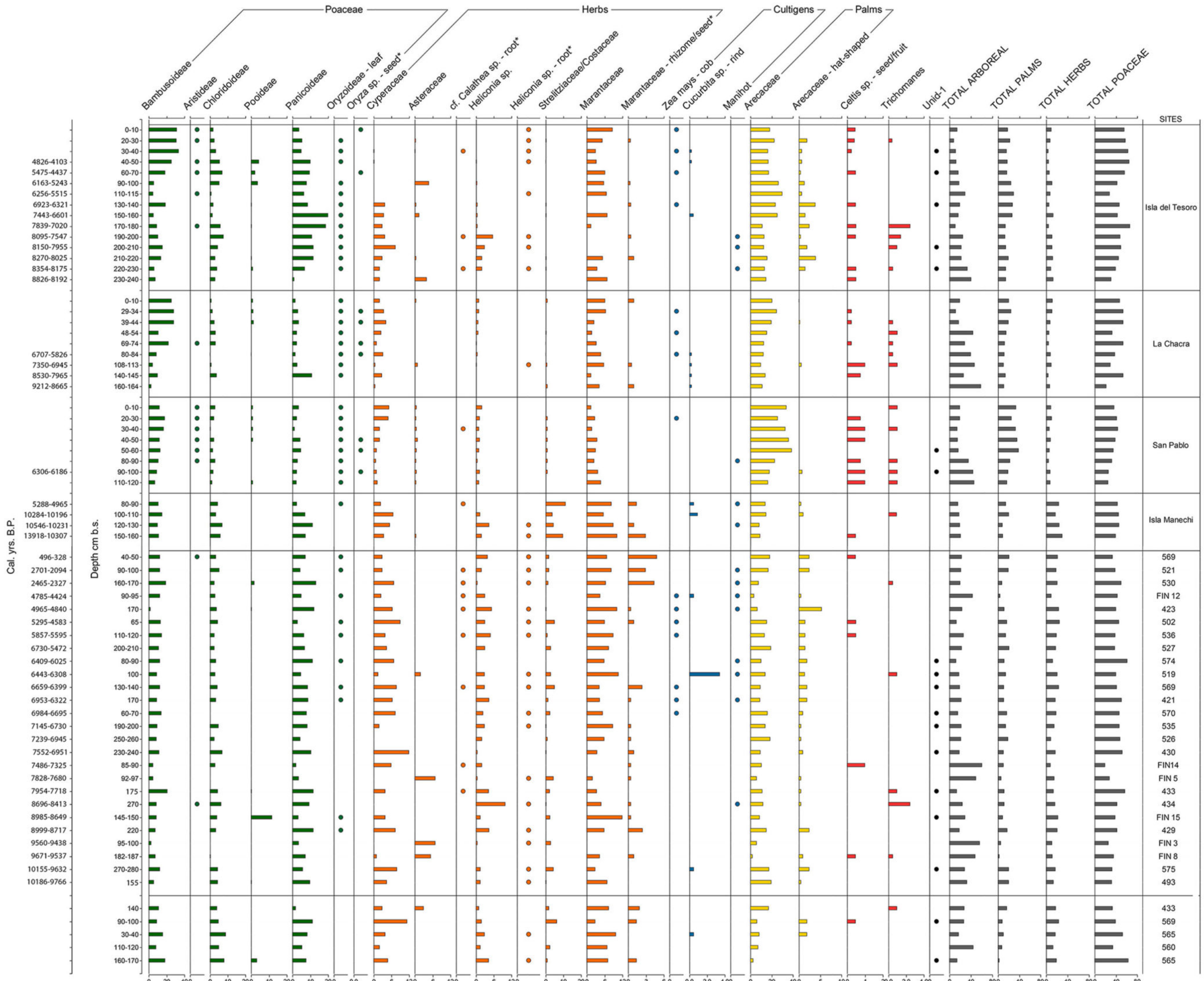

Fig. ED2.

Detailed percentage phytolith diagram for all the samples analyzed from anthropogenic FIs. *Non-domesticated, edible plants. Phytolith percentages are based on a minimum of 200 diagnostic phytoliths that were counted per slide

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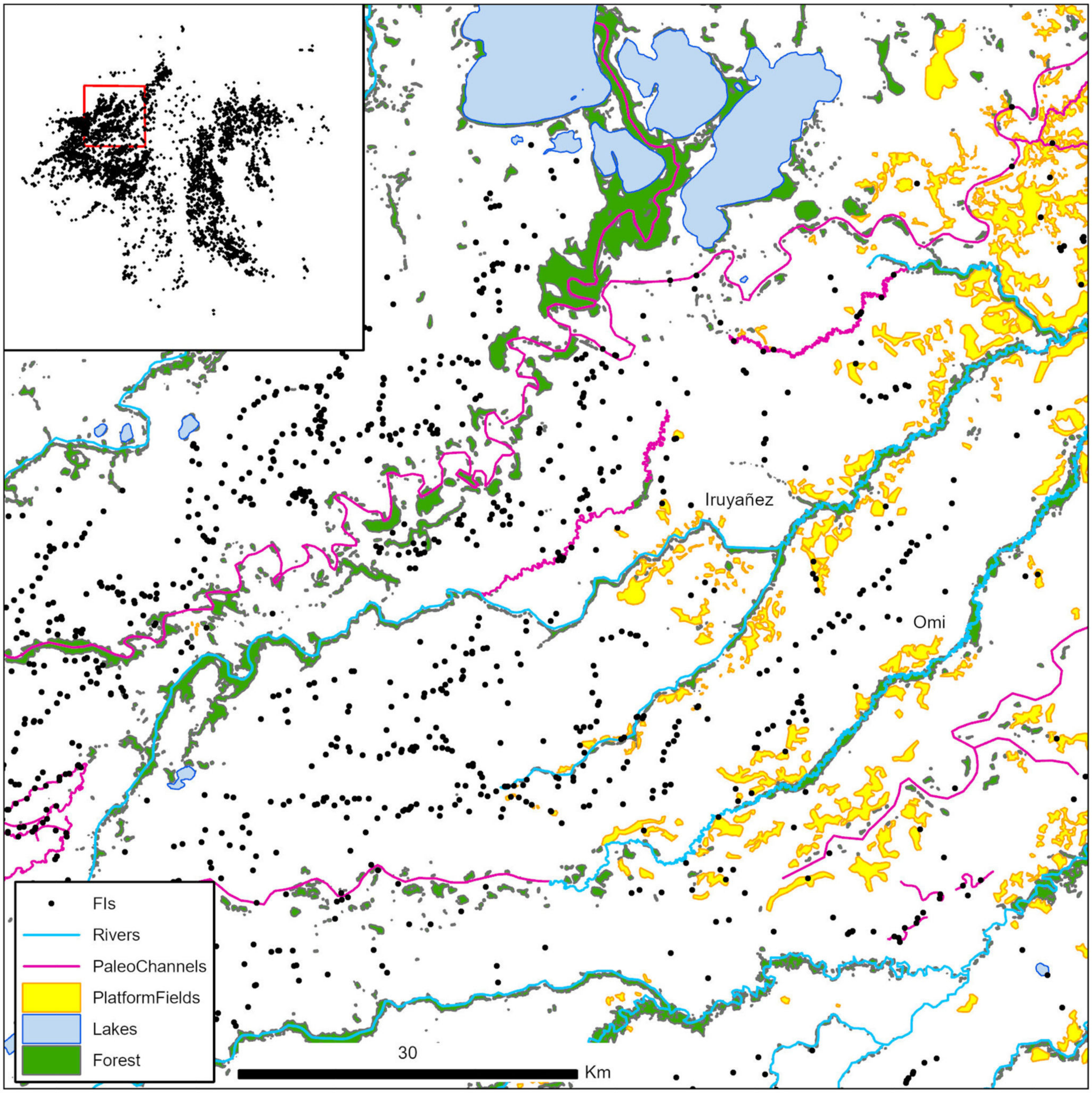

Fig. ED3.

Map of all the FIs and platform fields in a north-western subset of the LM. Platform fields are mostly built along paleochannels. Rivers Omi and Yruyañez flow inside old channels of the Beni River. FIs are mostly located in interfluvial areas. The region contains a total of 2428 patches of forest, 955 of which are FIs. Once all the patches of forest within a 2-km buffer of a river, paleoriver and lake are removed, FIs account for 60% of the remaining 1191 patches.

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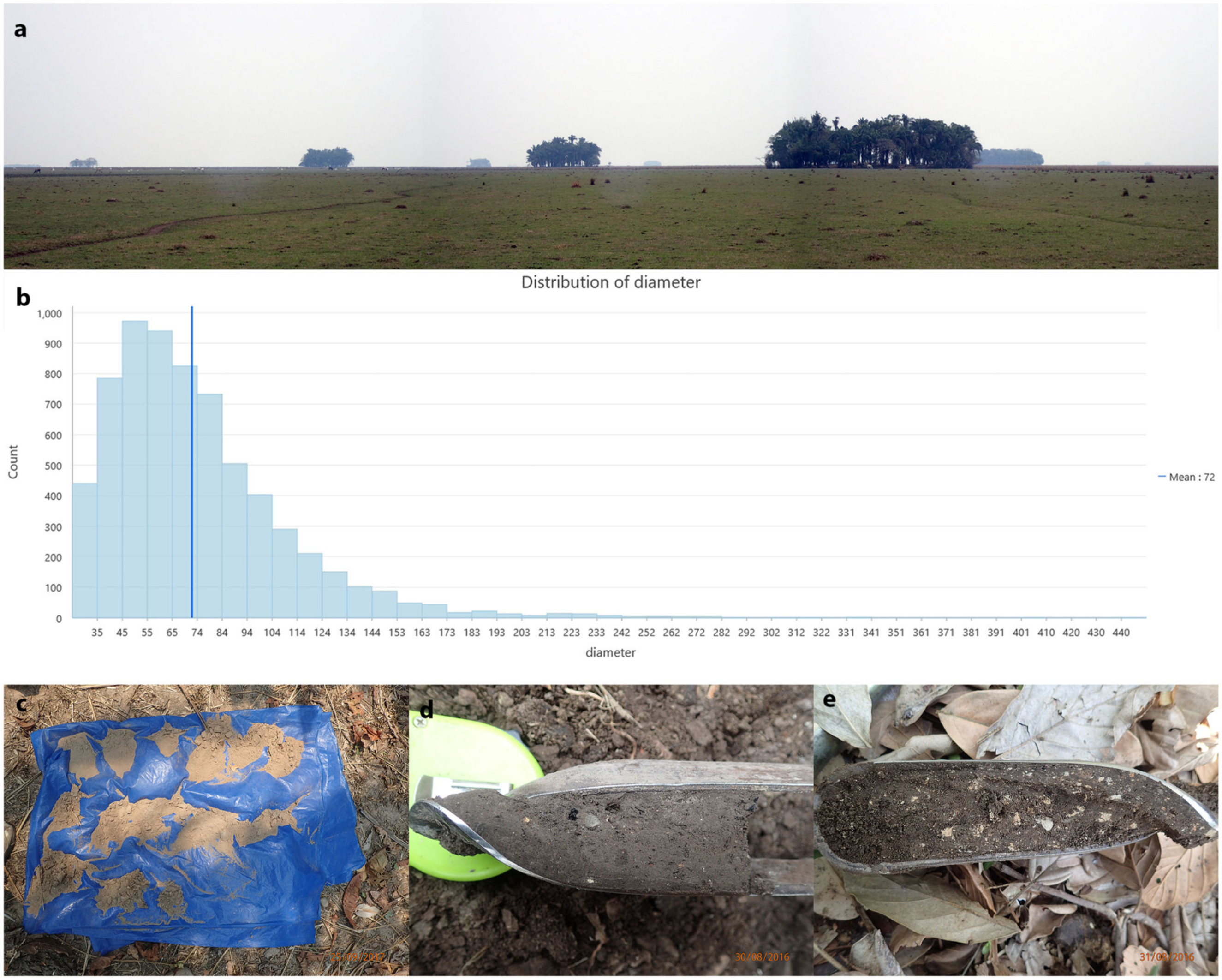

Fig. ED4.

Characteristics of FIs. a) Photo of the anthropic landscape dotted with forest islands in the Barba Azul Nature Reserve; b) Histogram showing the distribution of the diameter of FIs. The left side of the distribution is truncated at 25 m because smaller FIs have not been mapped; c) Photo taken at Site 579, natural FI. Samples are taken every 10 cm, from top left to down right. Material is silt with no organic matter; d) Photo taken at Site 425, anthropogenic FI. Depth of the sample 140 cm; e) Photo taken at Site 430, anthropogenic FI. Depth of the sample 160 cm. Samples in d) and e) are representative of the whole profile in site 425 and 430 respectively (see also Fig. ED7). We performed one core for each FI we visited.

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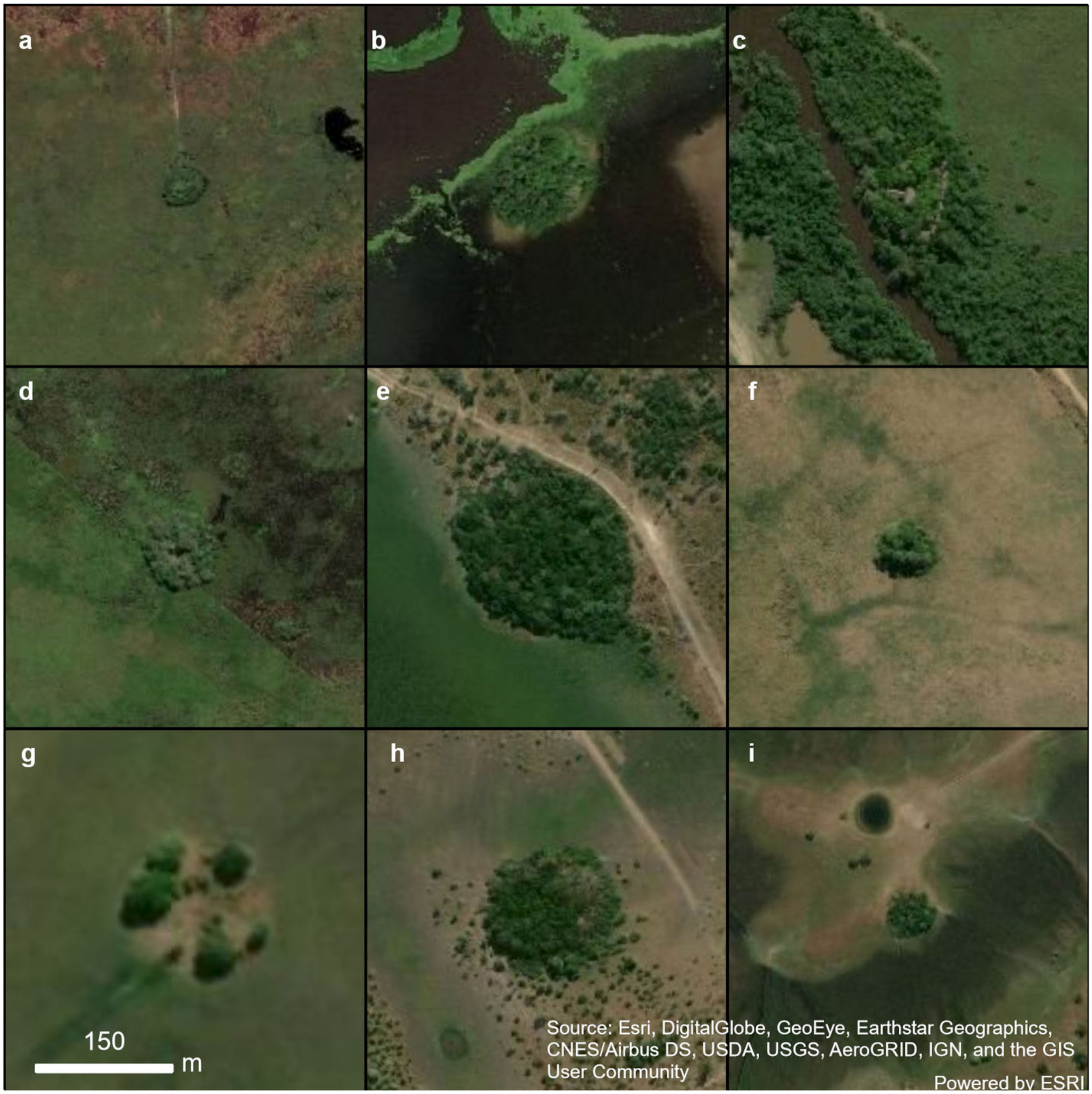

Fig. ED5.

Examples of surveyed FIs as seen in high-resolution satellite imagery of Esri ArcGIS basemap. a-f: FIs classified as anthropic (a, Sm4; b, Isla Manechi; c, Site 575; d, SM3; e, FIN 12; f, Isla del Tesoro); g-i: FIs classified as natural (g, FIN2; h, FIN11; I, Sire 529). Source: ESRI, DigitalGlobe, GeoEye, Earthstar Georaphics,CNES/Airbus DS.

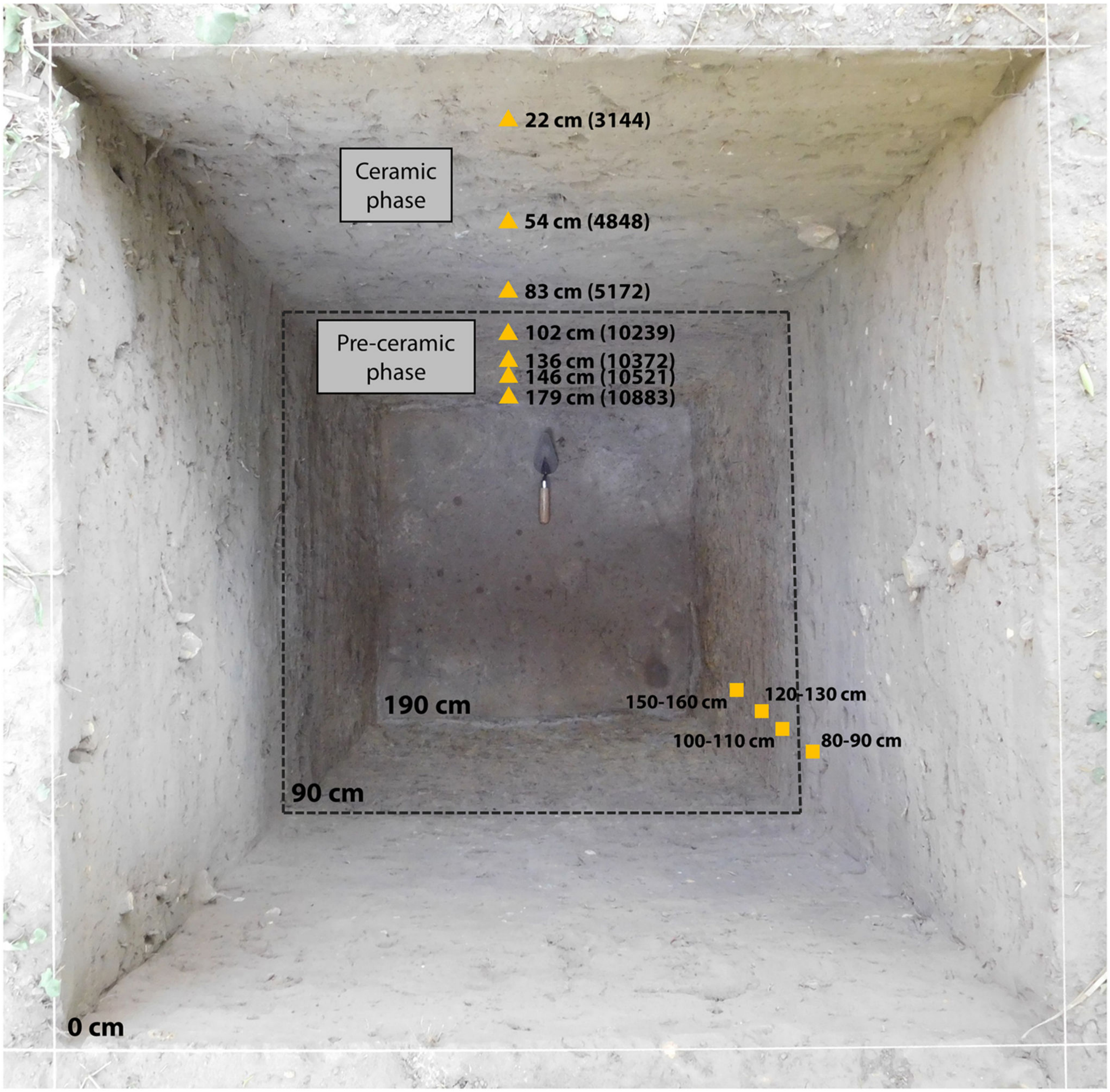

Fig. ED6.

Stratigraphic profile and sampling sites at Isla Manechi. Charcoal fragments for AMS 14C dating were collected during the excavation and yellow triangles indicate their depth. Yellow squares indicate the sampling locations of sediments analyzed for phytoliths, which have been sampled after the excavation from the vertical profile. The dashed line indicates the transition from the ceramic phase to the pre-ceramic one. This transition is characterized by a sharp increase in the compactness of sediments and amount of burnt earths. Values in parenthesis are median calibrated radiocarbon ages BP. A chronological gap of almost 4500 years exists between the two phases (Table ED1). All of these differences make it possible to exclude any contamination of phytoliths coming from the ceramic to the pre-ceramic contexts. For a description of archaeological excavations at Isla del Tesoro (SM1), La Chacra (SM3), and San Pablo (SM4) see Capriles et al.[13]

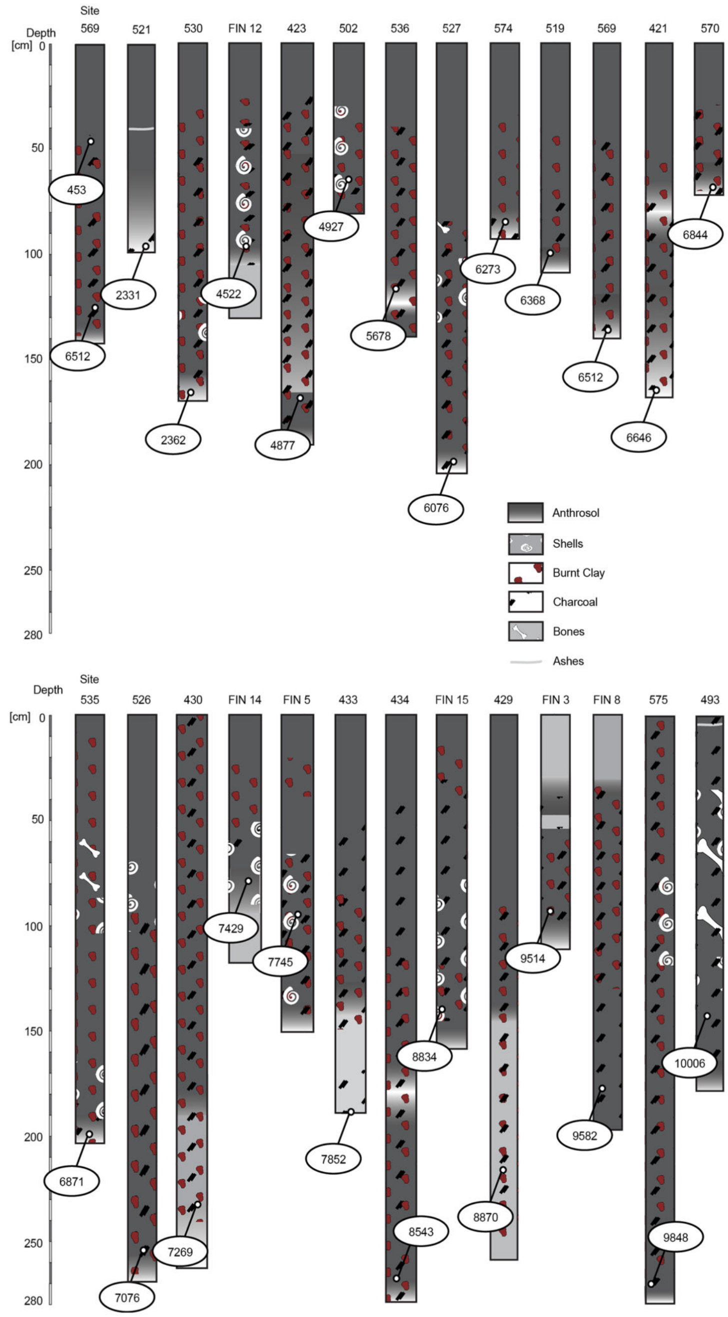

Fig. ED7.

Stratigraphic descriptions of cored sites. Radiocarbon dates are included in ovals as median calibrated years before present.

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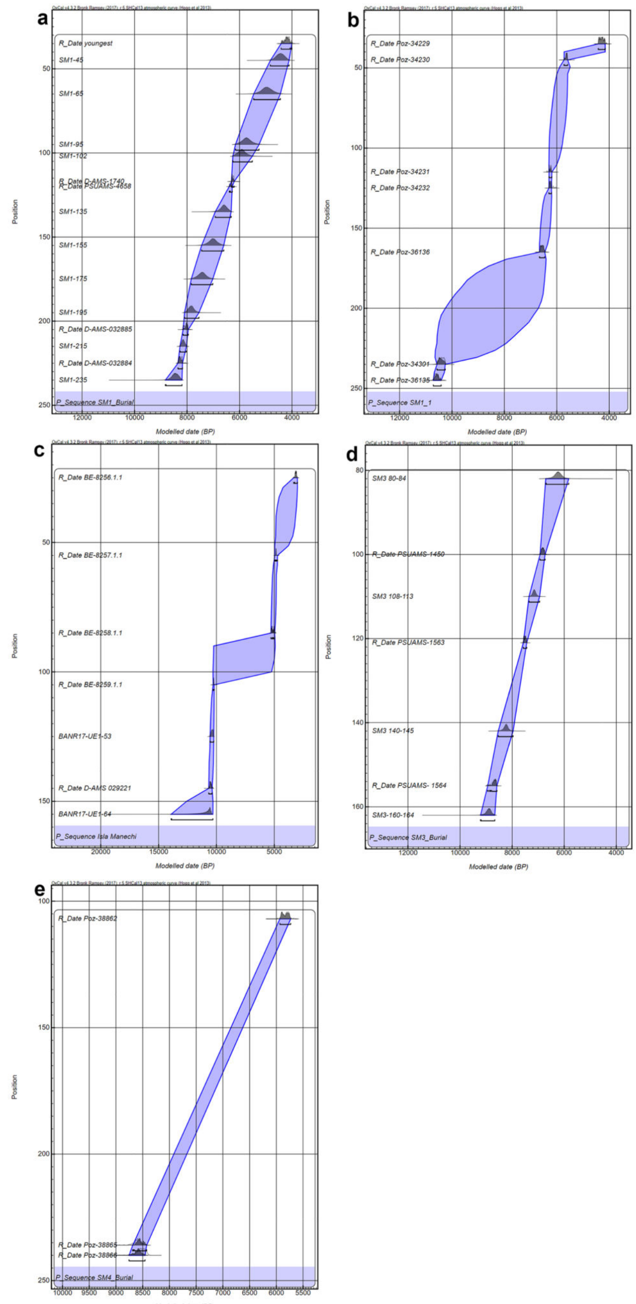

Fig. ED8.

Age-depth models of the modelled profiles. a) and b), Isla del Tesoro; c) Isla Manechi; d) and e) Isla La Chacra. The age-depth models have been produced using OxCal V4.3, code is available in Supplementary Information

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Table ED1

Radiocarbon ages of all the dated sites cited in the text including provenance and calibrations. Stratigraphically ordered dated depths have been modelled using a Bayesian age-depth model (OxCal 4.3's P_Sequence). The modelled ages for samples BANR17-UE1-53 and BANR17-UE1-64 have been calculated using the Date command. Code is available in Supplementary Information.

Lab _ Code	Site	14C BP	14C Age SD	Unmodelled (BP) 95.4%		Modelled (BP) 95.4%		Median	Material	Depth (cm)
				from	to	from	to			
D-AMS-1737	SM4, San Pablo	5476	35	6306	6124			6239	Bulk	58
Poz-46397	SM4, San Pablo	5190	80	6178	5664			5898	Charcoal	65
D-AMS-1741	SM4, San Pablo	5490	32	6306	6186			6245	Bulk	93
PSUAMS-4659	SM4, San Pablo	6665	25	7571	7441			7512	Charcoal	150
D-AMS-1739	SM4, San Pablo	6910	30	7787	7621			7696	Charcoal	150
Poz-46396	SM4, San Pablo	7700	90	8636	8218			8463	Charcoal	197
PSUAMS-1450	SM3, La Chacra	6030	30	6935	6736	6925	6734	6825	Charcoal	100
Poz-38862	SM3, La Chacra	5140	40	5930	5733	5933	5733	5825	Shell	107
PSUAMS-1563	SM3, La Chacra	6650	30	7566	7437	7568	7441	7506	Charcoal	121
PSUAMS-1564	SM3, La Chacra	7930	30	8972	8590	8951	8586	8672	Charcoal	155
Poz-38865	SM3, La Chacra	7860	50	8847	8435	8682	8426	8557	Shell	236
Poz-38866	SM3, La Chacra	7790	80	8760	8383	8748	8456	8590	Charcoal	240
Poz-38853	SM2, San Francisco	4950	40	5736	5585			5638	Shell	85
Poz-38850	SM2, San Francisco	4770	60	5588	5320			5465	Charcoal	155
Poz-38851	SM2, San Francisco	5380	40	6272	5994			6117	Shell	205
Poz-38852	SM2, San Francisco	5500	40	6393	6128			6253	Charcoal	205
Poz-34228	SM1, Isla del Tesoro	345	25	452	304			391	Bone	15
Poz-34229	SM1, Isla del Tesoro	3895	35	4411	4153	4414	4155	4292	Shell	35
Poz-34230	SM1, Isla del Tesoro	4945	35	5722	5586	5721	5585	5629	Shell	45
Poz-28854	SM1, Isla del Tesoro	3830	50	4405	3986			4172	Shell	48

Lab _ Code	Site	14C BP	14C Age SD	Unmodelled (BP) 95.4%		Modelled (BP) 95.4%		Median	Material	Depth (cm)
				from	to	from	to			
Poz-28855	SM1, Isla del Tesoro	4415	35	5210	4849			4937	Charcoal	77
Poz-22902	SM1, Isla del Tesoro	5520	40	6395	6190			6280	Charcoal	115
Poz-34231	SM1, Isla del Tesoro	5520	40	6395	6190	6295	6190	6234	Shell	115
Poz-24633	SM1, Isla del Tesoro	5360	40	6266	5950			6096	Shell	115
D-AMS-1740	SM1, Isla del Tesoro	5502	30	6310	6190	6309	6207	6275	Charcoal	117
PSUAMS-4658	SM1, Isla del Tesoro	5565	20	6398	6281	6393	6278	6305	Charcoal	120
Poz-24634	SM1, Isla del Tesoro	5505	35	6388	6184			6262	Charcoal	120
Poz-34232	SM1, Isla del Tesoro	5460	40	6304	6021	6302	6205	6254	Shell	125
Poz-28856	SM1, Isla del Tesoro	4480	40	5284	4872			5047	Charcoal	140
Poz-28850	SM1, Isla del Tesoro	4495	35	5288	4886			5109	Shell	140
Poz-36136	SM1, Isla del Tesoro	5800	35	6657	6453	6660	6461	6563	Charcoal	160
D-AMS 032885	SM1, Isla del Tesoro	7271	40	8162	7966	8151	7956	8019	Bulk orqanic	205
D-AMS 032884	SM1, Isla del Tesoro	7447	37	8348	8065	8347	8174	8274	Bulk orqanic	225
Poz-34301	SM1, Isla del Tesoro	9270	60	10556	10248	10573	10259	10434	Bulk orqanic	235
Poz-36135	SM1, Isla del Tesoro	9420	50	10743	10433	10715	10416	10574	Charcoal	245
BE-4254.1.1	FIN8_182-187	8681	22	9671	9537			9582	Charcoal	185
BE-4253.1.1	FIN5_92-97	6963	25	7828	7680			7745	Shell	95
BE-4250.1.1	FIN3_95-100	8572	48	9560	9438			9514	Charcoal	97
BE-4257.1.1	FIN15_145-150	7997	25	8985	8649			8834	Shell	147
BE-4256.1.1	FIN14_85-90	6552	25	7486	7325			7429	Shell	87
BE-4255.1.1	FIN12_90-95	4092	24	4785	4424			4522	Shell	92
BE-8256.1.1	BANR17-UE1-5	3017	21	3236	3005	3319	3007	3144	Charcoal	25
BE-8257.1.1	BANR17-UE1-20	4324	22	4959	4743	4957	4728	4848	Charcoal	55
BE-8258.1.1	BANR17-UE1-31	4491	23	5285	4888	5288	4965	5172	Charcoal	85
BE-8259.1.1	BANR17-UE1-38	9138	24	10367	10195	10284	10196	10239	Charcoal	105
	BANR17-UE1-53					10546	10231	10372		125

Lab _ Code	Site	14C BP	14C Age SD	Unmodelled (BP) 95.4%		Modelled (BP) 95.4%		Median	Material	Depth (cm)
				from	to	from	to			
D-AMS 029221	BANR17-UE1-57	9346	41	10653	10298	10664	10380	10521	Charcoal	145
	BANR17-UE1-64					13918	10307	10883		155
BE-7663.1.1	575_270-280	8849	50	10155	9632			9848	Charcoal	275
BE-7671.1.1	574_80-90	5516	62	6409	6025			6273	Charcoal	85
BE-7667.1.1	570_60-70	6046	48	6984	6695			6844	Charcoal	65
BE-7675.1.1	569_40-50	407	19	496	328			453	Charcoal	45
BE-7672,1.1	569_130-140	5759	53	6659	6399			6512	Charcoal	135
BE-7664.1.1	536_110-120	4994	37	5857	5595			5678	Charcoal	115
BE-7668.2.1	535_190-200	6069	51	7145	6730			6871	Charcoal	195
BE-7673.2.1	530_160-170	2397	20	2465	2327			2362	Charcoal	165
BE-7661.1.1	527_200-210	5337	281	6730	5472			6076	Charcoal	205
BE-7662.1.1	526_250-260	6217	40	7239	6945			7076	Charcoal	255
BE-7674.1.1	521_90-100	2346	89	2701	2094			2331	Charcoal	95
BE-7666.1.1	519_100	5647	22	6443	6308			6368	Charcoal	100
BE-6164.1.1	502 65	4365	110	5295	4583			4927	Charcoal	65
BE-6166.1.1	493 155	8920	49	10186	9766			10006	char/sed	155
BE-6153.1.1	490 95-100	3796	33	4237	3985			4115	Shell	97
BE-6167.1.1	434 270	7811	57	8696	8413			8543	char/sed	270
BE-6163.1.1	433 175	7058	50	7954	7718			7852	char/sed	175
BE-6168.1.1	430 235	6397	130	7552	6951			7269	chat/sed	235
BE-6158.1.1	429 220	8028	24	8999	8717			8870	char/sed	220
BE-6157.1.1	423 170	4365	21	4965	4840			4877	char/sed	170
BE-6159.1.1	421 170	5875	127	6953	6322			6646	char/sed	170

Table ED2

Length and thickness range and average size of scalloped-sphere phytoliths identified in this study. Based on Piperno et al. (2000), we consider scalloped spheres longer than 72 μm or thicker than 59 μm as coming from domestic varieties of Cucurbita sp.

Site	Date cal. yr. B.P.	Length (μm)	Thickness (μm)	Domesticated	Depth
Isla del Tesoro	7839-7020	80,361	59,804	Yes	170-180 cm
		82,524	58,318	Yes	
		72,804	65,178	Yes	
575	10155-9632	72,775	54,214	Yes	270-280 cm
		77,884	55,212	Yes	
519	6443-6380	82,418	65,752	Yes	100 cm

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Site	Date cal. yr. B.P.	Length (μm)	Thickness (μm)	Domesticated	Depth
		75,938	54,452	Yes	
		75,296	57,433	Yes	
		81.19	55,162	Yes	
		80,653	60,988	Yes	
		61,005	45,635	No	
FIN-12	4785-4424	77,871	67,843	Yes	90-95 cm
		83,697	59,724	Yes	
	6707-5826	78,895	52,993	Yes	80-84 cm
	7350-6945	75,789	56,754	Yes	108-113 cm
	8530-7965	63,119	41,238	No	140-145 cm
La Chacra	9212-8665	75,419	65,484	Yes	160-165 cm
		74.28	52.33	Yes	
		72.7	57.57	Yes	
		78.49	50.79	Yes	
		81.34	48.89	Yes	
		70.1	45.38	Yes	
		78.12	64.79	Yes	
		61.29	51	No	
		69.22	56.6	No	
		61.78	46.56	No	
	3319-3007	59.96	49.13	No	25 cm
		68.67	54.95	No	
		57.22	40.23	No	
		70.53	49.5	No	
		63.21	49.51	No	
		70.59	44.29	No	
		81.74	66.85	Yes	
	4957-4728	72.76	58.61	Yes	55 cm
		74.27	57.12	Yes	
		74.53	45.13	Yes	
		58.98	44.15	No	
		81.95	56.8	Yes	
		68.1	59.06	No	
		66.84	55.37	No	
		76.91	49.26	Yes	
		74.69	47.15	Yes	
	5288-4965	84.72	60.19	Yes	85 cm
		78,173	66,108	Yes	
Isla Manechi	10284-10196	84,996	67,836	Yes	105 cm

Site	Date cal. yr. B.P.	Length (µm)	Thickness (µm)	Domesticated	Depth
		72,601	54,422	Yes	
		64,201	50,158	No	
		84,858	64,479	Yes	
		68.44	57.37	No	
		81.82	60.62	Yes	
		86.81	63.17	Yes	
	10664-10380	60.46	51.16	No	145 cm

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

1. Larson G, et al. Current perspectives and the future of domestication studies. Proceedings of the National Academy of Sciences. 2014; 111:6139–6146. DOI: 10.1073/pnas.1323964111
2. Zohary, D, Hopf, M. Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe and the Nile Valley. Oxford University Press; 2000.
3. Zeder, MA, Bradley, DG, Smith, BD, Emshwiller, E. Documenting domestication: new genetic and archaeological paradigms. Univ of California Press; 2006.
4. Piperno, DR, Pearsall, DM. The origins of agriculture in the lowland Neotropics. 1998.
5. Piperno DR. The Origins of Plant Cultivation and Domestication in the New World Tropics: Patterns, Process, and New Developments. Current Anthropology. 2011; 52:S453–S470. DOI: 10.1086/659998
6. Clement CR, de Cristo-Araújo M, d'Eeckenbrugge GC, Alves Pereira A, Picanço-Rodrigues D. Origin and Domestication of Native Amazonian Crops. Diversity. 2010; 2:72–106. DOI: 10.3390/d2010072
7. Olsen KM, Schaal BA. Microsatellite variation in cassava (Manihot esculenta, Euphorbiaceae) and its wild relatives: further evidence for a southern Amazonian origin of domestication. Am J Bot. 2001; 88:131–142. [PubMed: 11159133]
8. Sanjur OI, Piperno DR, Andres TC, Wessel-Beaver L. Phylogenetic relationships among domesticated and wild species of *Cucurbita* (Cucurbitaceae) inferred from a mitochondrial gene: Implications for crop plant evolution and areas of origin. Proceedings of the National Academy of Sciences. 2002; 99:535.doi: 10.1073/pnas.012577299

Europe PMC Funders Author Manuscripts

9. Clement CR, et al. The domestication of Amazonia before European conquest. Proceedings of the Royal Society of London B: Biological Sciences. 2015; 282doi: 10.1098/rspb.2015.0813
10. Scaldaferro MA, Barboza GE, Acosta MC. Evolutionary history of the chili pepper Capsicum baccatum L. (Solanaceae): domestication in South America and natural diversification in the Seasonally Dry Tropical Forests. Biological Journal of the Linnean Society. 2018; 124:466–478. DOI: 10.1093/biolinnean/bly062
11. Watling J, et al. Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. PLoS ONE. 2018; 13:e0199868.doi: 10.1371/journal.pone.0199868 [PubMed: 30044799]
12. Lombardo U, et al. Early and Middle Holocene Hunter-Gatherer Occupations in Western Amazonia: The Hidden Shell Middens. PLoS ONE. 2013; 8:e72746.doi: 10.1371/journal.pone.0072746 [PubMed: 24013964]
13. Capriles JM, et al. Persistent Early to Middle Holocene tropical foraging in southwestern Amazonia. Science Advances. 2019; 5doi: 10.1126/sciadv.aav5449
14. Hilbert L, et al. Evidence for mid-Holocene rice domestication in the Americas. Nature Ecology & Evolution. 2017; 1:1693–1698. DOI: 10.1038/s41559-017-0322-4 [PubMed: 28993622]
15. Lombardo U, et al. Holocene land cover change in south-western Amazonia inferred from paleoflood archives. Global and Planetary Change. 2019; 174:105–114. DOI: 10.1016/j.gloplacha.2019.01.008
16. Chandler-Ezell K, Pearsall DM, Zeidler JA. Root and tuber phytoliths and starch grains document manioc (Manihot esculenta) arrowroot (Maranta arundinacea) and llerén (Calathea sp.) at the real alto site Ecuador. Economic Botany. 2006; 60:103–120.
17. Piperno, DR. Phytoliths. AltaMira Press; 2006.
18. Morcote-Ríos G, Bernal R, Raz L. Phytoliths as a tool for archaeobotanical, palaeobotanical and palaeoecological studies in Amazonian palms. Botanical Journal of the Linnean Society. 2016; 182:348–360. DOI: 10.1111/boj.12438
19. Hanelt, P, Buttner, R, Mansfeld, R. Mansfeld's Encyclopedia of Agricultural and Horticultural Crops (except Ornamentals). Springer; 2001.
20. Smith BD. The Initial Domestication of *Cucurbita pepo* in the Americas 10,000 Years Ago. Science. 1997; 276:932–934. DOI: 10.1126/science.276.5314.932
21. Piperno DR, Stothert KE. Phytolith Evidence for Early Holocene Cucurbita Domestication in Southwest Ecuador. Science. 2003; 299:1054–1057. DOI: 10.1126/science.1080365 [PubMed: 12586940]
22. Dillehay, TD, Piperno, DR. The Cambridge World Prehistory. Renfrew, C, Bahn, P, editors. Cambridge University Press; 2014. 970–985.
23. Kistler L, et al. Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. Science. 2018; 362:1309–1313. DOI: 10.1126/science.aav0207 [PubMed: 30545889]
24. Rival L, McKey D. Domestication and diversity in manioc (*Manihot esculenta* Crantz ssp. *esculenta*, Euphorbiaceae). Current Anthropology. 2008; 49:1119–1128.
25. Rodrigues L, Lombardo U, Veit H. Design of pre-Columbian raised fields in the Llanos de Moxos, Bolivian Amazon: Differential adaptations to the local environment? Journal of Archaeological Science: Reports. 2018
26. Junqueira AB, Shepard GH, Clement CRJEB. Secondary Forests on Anthropogenic Soils of the Middle Madeira River: Valuation, Local Knowledge, and Landscape Domestication in Brazilian Amazonia. 2011; 65:85–99. DOI: 10.1007/s12231-010-9138-8
27. McKey D, Cavagnaro TR, Cliff J, Gleadow RJC. Chemical ecology in coupled human and natural systems: people, manioc, multitrophic interactions and global change. 2010; 20:109–133. DOI: 10.1007/s00049-010-0047-1
28. Jones, M. The Evolution of Hominin Diets. Springer; 2009. 171–180.
29. Aceituno FJ, Loaiza N. The origins and early development of plant food production and farming in Colombian tropical forests. Journal of Anthropological Archaeology. 2018; 49:161–172. DOI: 10.1016/j.jaa.2017.12.007

Europe PMC Funders Author Manuscripts

30. Smith BD. General patterns of niche construction and the management of 'wild' plant and animal resources by small-scale pre-industrial societies. Philosophical Transactions of the Royal Society B: Biological Sciences. 2011; 366:836–848. DOI: 10.1098/rstb.2010.0253
31. Lombardo U, May J-H, Veit H. Mid- to late-Holocene fluvial activity behind pre-Columbian social complexity in the southwestern Amazon basin. The Holocene. 2012; 22:1035–1045. DOI: 10.1177/0959683612437872
32. Manning AD, Fischer J, Lindenmayer DB. Scattered trees are keystone structures – Implications for conservation. Biological Conservation. 2006; 132:311–321. DOI: 10.1016/j.biocon.2006.04.023
33. Tews J, et al. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography. 2004; 31:79–92. DOI: 10.1046/j.0305-0270.2003.00994.x
34. Berkunsky I, et al. Assessing the use of forest islands by parrot species in a neotropical savanna. Avian Conservation and Ecology. 2015; 10:11.
35. Prümers H, Jaimes Betancourt C. 100 años de investigación arqueológica en los Llanos de Mojos. Arqueoantropológicas. 2014; 4:11–53.
36. Lombardo U, Canal-Beeby E, Veit H. Eco-archaeological regions in the Bolivian Amazon: Linking pre-Columbian earthworks and environmental diversity. Geographica Helvetica. 2011; 66:173–182.
37. Langstroth RP. Biogeography of the Llanos de Moxos: natural and anthropogenic determinants. Geographica Helvetica. 2011; 66:183–192.
38. Lombardo U, Denier S, Veit H. Soil properties and pre-Columbian settlement patterns in the Monumental Mounds Region of the Llanos de Moxos, Bolivian Amazon. SOIL. 2015; 1:65–81. DOI: 10.5194/soil-1-65-2015
39. Rodrigues L, Lombardo U, Canal Beeby E, Veit H. Linking soil properties and pre-Columbian agricultural strategies in the Bolivian lowlands: The case of raised fields in Exaltación. Quaternary International. 2017; 437(Part B):143–155. DOI: 10.1016/j.quaint.2015.11.091
40. Boixadera J, Poch RM, García-González MT, Vizcayno C. Hydromorphic and clay-related processes in soils from the Llanos de Moxos (northern Bolivia). Catena. 2003; 54:403–424. DOI: 10.1016/s0341-8162(03)00134-6
41. Hanagarth, W. Acerca de la geoecología de las sabanas del Beni en el noreste de Bolivia. Instituto de ecología; 1993.
42. Lombardo U, Ruiz-Pérez J, Madella M. Sonication improves the efficiency, efficacy and safety of phytolith extraction. Review of Palaeobotany and Palynology. 2016; 235:1–5. DOI: 10.1016/j.revpalbo.2016.09.008
43. Piperno DR. Identifying crop plants with phytoliths (and starch grains) in Central and South America: A review and an update of the evidence. Quaternary International. 2009; 193:146–159. DOI: 10.1016/j.quaint.2007.11.011
44. Iriarte J. Assessing the feasibility of identifying maize through the analysis of cross-shaped size and three-dimensional morphology of phytoliths in the grasslands of southeastern South America. Journal of Archaeological Science. 2003; 30:1085–1094.
45. Watling J, et al. Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions II: Southwestern Amazonian forests. Review of Palaeobotany and Palynology. 2016; 226:30–43. DOI: 10.1016/j.revpalbo.2015.12.002
46. Dickau R, et al. Differentiation of neotropical ecosystems by modern soil phytolith assemblages and its implications for palaeoenvironmental and archaeological reconstructions. Review of Palaeobotany and Palynology. 2013; 193:15–37. DOI: 10.1016/j.revpalbo.2013.01.004
47. Hogg AG, et al. SHCal13 Southern Hemisphere Calibration, 0–50,000 Years cal BP. Radiocarbon. 2013; 55:1889–1903.
48. Bronk Ramsey C. Bayesian Analysis of Radiocarbon Dates. Radiocarbon. 2009; 51:337–360. DOI: 10.1017/S0033822200033865

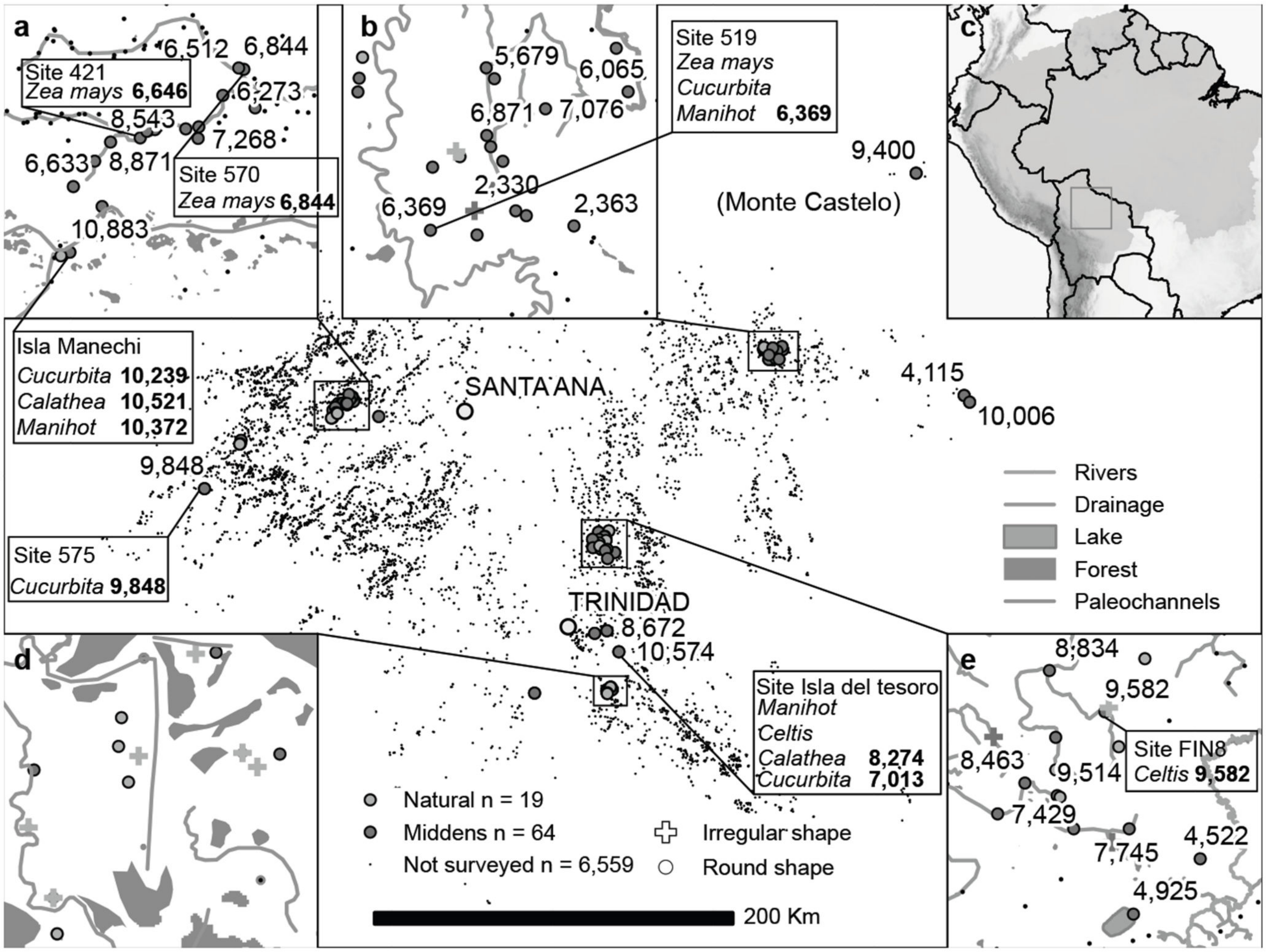

Figure 1.

Forest islands mapped in the LM. Numbers associated with middens are ages expressed in median cal yr BP from the deepest anthropic datable layer at each site (Table ED1). Insets a, b, d and e identify the four areas that were surveyed to estimate the total number of anthropic FIs in the LM (Fig. ED1). The square in inset c identifies the study area; the shaded area in inset c depicts Greater Amazonia.

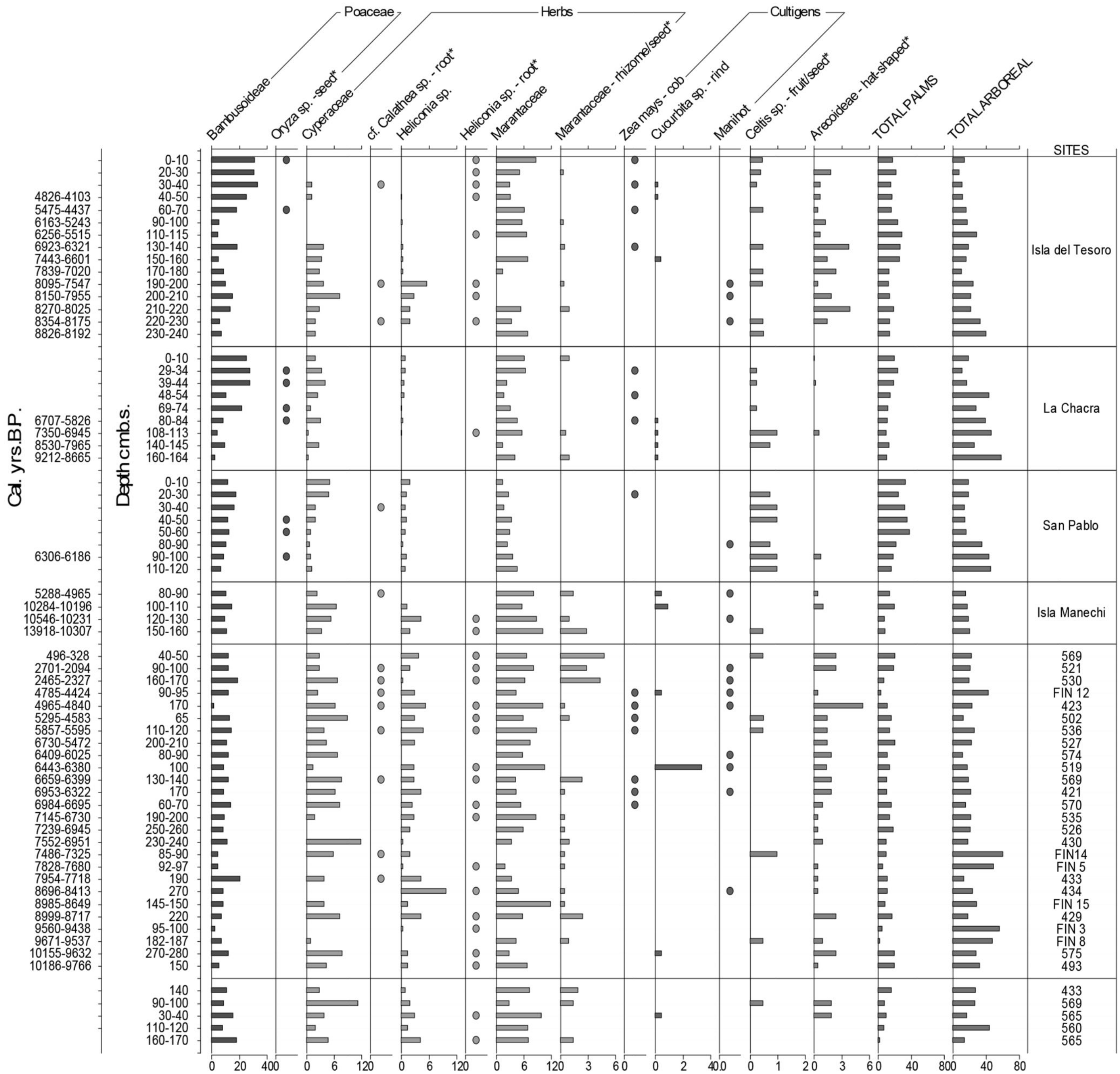

Figure 2.

Diagram showing the percentage of most relevant phytolith groups from anthropic forest islands. Dots indicate presence ≤ 1% (for more details see Fig. ED2 and table ED1). *Non-domesticated, edible plants (used as food resources)[26]. Phytolith percentages are based on a minimum of 200 diagnostic phytoliths counted per slide.

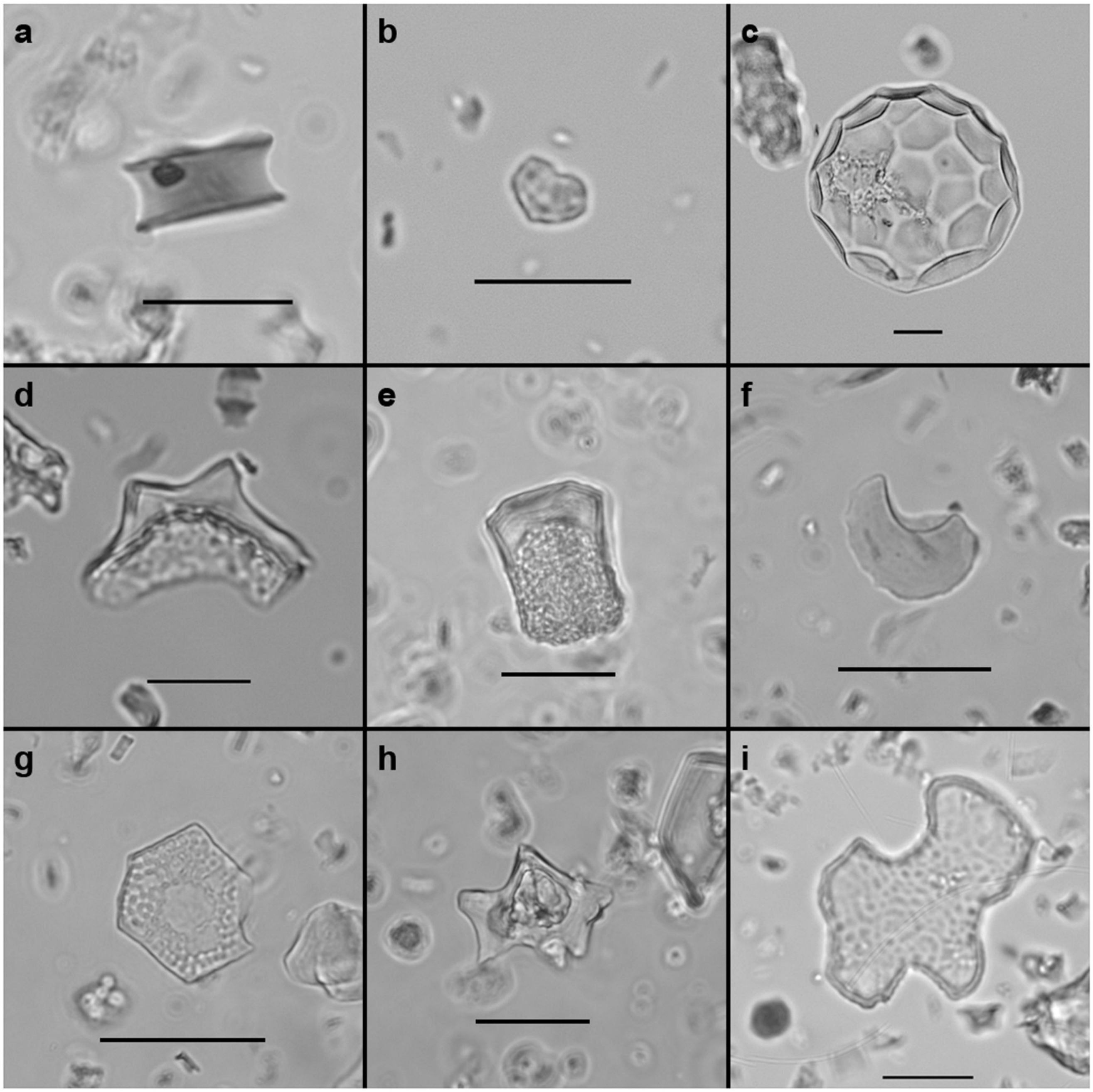

Figure 3.

Photomicrographs of phytolith morphotypes recovered from Isla del Tesoro, La Chacra and Isla Manechi: (a) wavy-top rondel from the cob of maize (Zea mays) (sampleIT190-200); (b) heart-shaped phytolith from the secretory cells of manioc (Manihot) (sample BANR17-UE1-57); (c) scalloped sphere from the rind of squash (Cucurbita sp.) (sample BANR17-UE1-31); (d) double-peaked glume from the seed of rice (Oryza sp.) (sample SM3-116s); (e) flat domed cylinder from the rhizome of Calathea sp. (sample IT30-40); (f) short trough body from the rhizome of Heliconia sp. (sample IT130-140); (g) stippled polygonal body from the seed of Cyperaceae (sample IT150-170); (h) nodular projections with a pointed apex phytolith from the seed of Marantaceae (sampleIT90-100) (i) stippled plate from the seed/fruit of hackberries (Celtis sp.) (sample SM3-69-74). Scale bars = 20µm.