Legacies of Indigenous Land use and Cultural Burning in the Bolivian Amazon

Rainforest Ecotone

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Abstract

The southwestern Amazon Rainforest Ecotone (ARE) is the transitional landscape between the tropical forest and seasonally flooded savannahs of the Bolivian Llanos de Moxos. These heterogeneous landscapes harbor high levels of biodiversity and some of the earliest records of human occupation and plant domestication in Amazonia. While persistent Indigenous legacies have been demonstrated elsewhere in the Amazon, it is unclear how past human-environment interactions may have shaped vegetation composition and structure in the ARE. Here, we examine 6000 years of archaeological and palaeoecological data from Laguna Versalles (LV), Bolivia. LV was dominated by stable rainforest vegetation throughout the Holocene. Maize cultivation and cultural burning are present after ~5,700 cal yr BP. Polyculture of maize, manioc, and leren after ~3400 cal yr BP predates the formation of Amazonian Dark/Brown Earth (ADE/ABE) soils (~2400 cal yr BP). ADE/ABE formation is associated with ceramics, record levels of burning, and increased edible palms including Mauritia flexuosa and Attalea. Frequent cultural burning altered ADE/ABD forest composition and structure by controlling ignitions, decreasing fuel loads, and increasing the abundance of plants preferred by humans. Polyculture agroforestry was a stable subsistence strategy that persisted despite pronounced climate change and cultural transformations and has an enduring legacy on ADE/ABE forests in the ARE.

Introduction

The Amazon Rainforest Ecotone (ARE) of the southwestern rim of the Amazon Basin is a transitional landscape between the tropical forests (i.e. *terra firme* rainforest: TFRF) and the seasonally flooded savannahs (SFS)[1] of the Llanos de Moxos. The ARE harbors high-levels of habitat heterogeneity and biodiversity [1] and the SFS harbor some of the earliest records of human occupation and plant domestication in the Amazon [2-6]. Today, fire plays an integral role in maintaining the ARE boundary between fireadverse rainforest vegetation with infrequent incidence of fire and fire-adapted savannah vegetation with frequent fire occurrence [7,8]. However, the long-term fire history (>centennial time-scale), the response of fire to climate change, and the ecological impacts of natural- and human-caused ignitions in the ARE remain largely unknown [9-11]. In the upcoming century, regional precipitation is expected to decrease as a result of deforestation and reduced evapotranspiration, while natural- and human-caused ignitions are projected to increase fire activity in the ARE [12-14]. As a consequence of these knowledge gaps the ARE has largely been neglected in fire management strategies and conservation initiatives.

Recent studies indicate Indigenous land use and traditional burning practices (henceforth cultural burning [15]) influenced composition and structure in the Amazon rainforests for millennia [6,16–22], particularly during the height of pre-Columbian Indigenous occupation in the Amazon [23–25] and earthwork construction (after ~2500 cal yr BP) [26–31]. Cultural burning is one of the most powerful tools used to transform landscapes [32–36]. It has been used to clear land for the creation of public, domestic and agricultural space, for slash and burn cultivation [37–39], for cooking and to burn

waste [17,40,41]. Additionally, the charcoal produced through cultural burning enhanced soil fertility in the formation of Amazonian Dark Earth (ADE) and Amazonian Brown Earth (ABE) soils [42–45].

The frequent use of cultural burning associated with Indigenous polyculture and ADE/ABE formation [44,46] influenced key components of the palaeofire regime, such as fire severity, fire frequency, and fire intensity [47]. Management practices involving fire altered forest composition and structure by promoting nutrient-demanding species, reducing competition for cultivated plants, reducing fuel loads, and increasing light availability [40,48]. Many plants, such as palms (i.e. *Mauritia* and *Attalea*), have evolved fire adaptations that enable them to persist through time in frequently burnt locations [49], increasing the abundance of fire tolerant plants while decreasing fire intolerant seed banks [50–60].

Persistent Indigenous legacies from cultural burning have been demonstrated elsewhere in Amazon rainforest ecosystems [16,20,61,62]; however, it is unclear how past human-environment interactions may have shaped transitional ecosystems associated with the ARE. To explore the influence of the past 6000 years of climate and human land use and cultural burning on ARE ecosystems in the Bolivian Amazon, we implemented a multi-proxy approach [63–65] to compare local-scale land use, vegetation, and fire histories (archaeological excavations/terrestrial archaeobotany) with broader regional-scale vegetation histories (lake palaeoecology). These data are contextualized with existing regional archaeological evidence documenting human occupation and plant domestication in the region as early as 10,500 cal yr BP [2,3,5], followed by a progressive late Holocene expansion in human occupation [23–25] and investment in landscape construction, including ring-ditches, causeways, ditched agricultural fields, and fish weirs

[66–69]. Additionally, the archaeological and palaeoecological data from Laguna Versalles (LV) are compared with palaeoclimate data from Pumacocha (~1300 km west of LV) [70], to contextualize the regional climate variability, including periods drier than present, such as the Mid-Holocene Dry Period (6000-4000 cal yr BP) and the Medieval Climate Anomaly (MCA) (1300-900 cal yr BP), and periods wetter than present, such as the Little Ice Age (LIA) [71,72].

Materials and Methods

Study Site

We selected the Iténez Forest Reserve, a ~5000-km² tract of forest located on the Precambrian Shield in the north east of Beni Department, Bolivia, surrounded to the east, south and west by seasonally flooded savannahs. The climate is seasonally dry, intertropical humid with a distinct wet season between November and March [73]. The mean annual rainfall is 1300 mm per year and the annual temperatures range between 23 °C and 27 °C [73]. The region is an ecological transition zone between *terra firme* (non-flooded) dense-canopy, humid evergreen rainforest floristically linked to the Madeira-Tapajos ecoregion [74,75], and the savannahs of the Beni Basin (135,000 km²) to the south. The archaeology of the Iténez region is characterized by extensive networks of earthworks that include ring-ditches, causeways, ditched agricultural fields, and fish weirs [66–69].

Research was conducted in and around Laguna Versalles, a large (~21.6 km²), closed-basin, flat-bottomed lake, located ~3 km southwest of the modern village of Versalles (12.66°S, 63.38°W; ~146 m above sea level) (Fig. 1). Versalles is located on the banks of the Iténez River (known as the Guaporé River in Brazil), within the tropical

forest on the northern border of the forest reserve. Today, Versalles is inhabited by an Itonama Indigenous community, which is built atop a pre-Columbian Indigenous settlement [76]. Archaeological and terrestrial palaeoecological research was conducted at the Triunfo site on the southwestern shore of Laguna Versalles, which includes a mosaic of anthropogenically enriched ADE/ABE soils surrounded by a ditch and embankment earthwork, known as a *zanja*, and a double ditch ring village [76].

To aid in archaeological and palaeoecological interpretations of past vegetation change, a vegetation transect survey was conducted across the Triunfo site, from the lake shore to offsite of the western boundary of Triunfo. All live trees, palms and lianas with a diameter at breast height (~1.30 m above the ground) larger or equal to 10 cm were measured within 10 m of the transect line (SOM Table 1). Field identifications along with voucher specimens were collected and transferred to the collections at the Santa Cruz Herbarium where taxonomic identifications were confirmed by specialists.

Palaeoecology

In 2016 a 42 cm sediment core dating to ~11,300 cal yr BP was collected from Laguna Versalles (LV) (12.42.45.6°S, 63.26.37.2°W; ~600 m from shore at 2.2 m depth), (Fig. 1A-B). Samples were taken from an anchored floating platform near the southwestern shore of the archaeological site of Triunfo, using a drop-hammer Colinvaux-Vohnout modified Livingston piston corer [77,78] with 5 cm diameter, 1.22 m aluminum tubes. The surface core was collected with a 5 cm diameter clear plastic tube to capture the uppermost unconsolidated sediments. Softer sediments from the surface core were divided in the field into 0.5 cm increments and stored in watertight plastic sample bags, with the remaining firmer sediments preserved in the aluminum tubes for transport to the

laboratory. All sediments were transported to the University of Exeter in the United Kingdom and stored at 4 °C.

Age Model

Age-depth relationships were modeled on five bulk sediment AMS radiocarbon dates (SOM Table 2) in a Bayesian framework using 'BACON' [79]. Dates were modelled using the IntCal20 Northern Hemisphere calibration curve [80]. IntCal20 was selected in place of the SHCal20 calibration curve [81] because of the latitudinal location of LV and the proximal hydrologic connection with the origin of the South American monsoon in the Northern Hemisphere. The seasonal migration of the ITCZ is thought to introduce a Northern Hemisphere ¹⁴C signal to the low-latitude Southern Hemisphere [82]. As LV is located in the low latitudes (12.7°S) and within the range of the ITCZ migration, the IntCal20 Northern Hemisphere calibration curve was selected for the radiocarbon calibrations. Radiocarbon ages were calibrated within Bacon v2.2 [83] in R [84–86]. The age-depth model mean accumulation rate priors were calculated using the 14C chronology (acc.mean = 200) and memory priors (mem.strength = 10; mem.mean = 0.3) (Fig. 2 SOM).

Pollen analysis

The LV sediment core was subsampled for pollen analysis at 2 cm intervals between 0 and 42 cm depth. Subsampled material (1 cm³) was prepared using a standard digestion protocol [87] including an additional sieving stage to concentrate large cultigen pollen types, such as maize (*Zea mays*), manioc (*Manihot esculenta*) and sweet potato (*Ipomoea batatas*) [88]. Fossil pollen was identified with reference to the collection of tropical pollen specimens housed at the University of Exeter and from the Amazon Pollen Manual and Atlas [78]. Pollen taxa were grouped into trees-shrubs, palms, herbs, and crops in the pollen diagram. Maize pollen grains were distinguished from those of other wild grasses using morphological and size criteria defined by Holst et al. (2007) [89]. Pollen types of cultigens and wild relatives of *I. batatas* are indistinguishable, but we are confident that the grains we report come from cultigens because (1) wild species of these crops were absent in the botanical survey conducted around the lake where these large, heavy pollen grains are most likely to originate, (2) the co-occurrence of *Ipomoea* and maize pollen, and (3) the absence of *Ipomoea* pollen in the record before the first signs of human land use. Thus, we interpret the results as evidence for sweet potato and maize cultivation.

Macrocharcoal

The LV sediment core was subsampled for macroscopic charcoal analysis at 0.5 cm intervals from 0 to 42 cm in depth. Samples were analyzed for charcoal pieces greater than 125 µm using a modified macroscopic sieving method [90]. Subsampled material (1 cm³) was treated with 5% potassium hydroxide in a hot water bath for 15 min. The residue was sieved through a 125 µm sieve. Macroscopic charcoal (particles of > 125 µm in diameter) was counted in a gridded petri dish at 40 x magnification on a dissecting microscope. Charcoal counts were converted to charcoal concentration (the number of charcoal particles cm⁻²) and charcoal accumulation rates by dividing by the deposition time (yr cm⁻¹). Charcoal influx data (particles cm⁻²yr⁻¹) were used as an indicator of fire severity (the amount of biomass consumed during a fire episode). CHAR statistical software was used to decompose charcoal data into signal-to-noise to identify distinct

charcoal peaks using standard methodology [91,92]. Charcoal peaks are interpreted as a fire episode. The time difference between peaks is reflected in the fire frequency (fire return interval) for every 1000 years.

Archaeology

A 4-week archaeological excavation was conducted in 2017 at the archaeological site of Triunfo located on the southwest shore of LV (Fig. 1) to recover cultural material and establish construction chronology of earthworks, and assess site formation history [76]. Ceramic material was analyzed following standard procedures to assess changes in form, paste, and decoration, and compared to regional collections (Fig. 1SOM). A transect of soil test pits, running perpendicular from the lake, were assessed for cultural materials, and the presence, depth and intensity of anthropogenic soil. Three soil test pits were excavated along the transect for archaeobotanical, geochemical, and isotopic sampling representing ADE, ABE, and nearby ferralsol soils used as control sample [76]. Archaeobotanical analysis of the samples (phytoliths and macrocharcoal) was conducted following standard procedures [65,76]. Full archaeobotanical analysis is presented elsewhere [5,76], with key results being discussed below.

Sum of Probability Distribution and Archaeological Site Frequency

Sum Probability Distributions (SPDs) were constructed from regional radiocarbon dates as a proxy for past activity following standard protocols and chronometric hygiene. SPDs were built in OxCal using the sum function and the IntCal20 calibration curve [80,93] with a data set of 39 radiocarbon dates from northeastern Bolivia (Fig. 1; SOM Table 3). To account for oversampling of some sites and phases within those sites, we applied a binning procedure [94,95]. Dates within sites were ordered and those occurring within 100 years of each other were grouped into bins and merged with the R_combine function. Despite the decrease in sample size, the filtered SPD is highly correlated with an SPD built with all radiocarbon dates (r2 = 0.991, P < 0.001). In addition to the SPD, a histogram of the number of occupied sites is used as another proxy of human activity, based on the medians of the calibrated dates per 200-year intervals. Although the radiocarbon record is inherently biased by research (privileged dating of certain sites or periods) and taphonomic factors (greater preservation of charcoal towards more-recent periods), SPDs have been shown to be a useful method to assess past population dynamics in relative terms, provided an adequate sample size and measures of chronometric hygiene [95,96], which were used here.

Results

To contextualize the history of human-environment interactions at Versalles, the palaeoecological and archaeobotanical reconstructions for the last ~6000 years are interpreted alongside a new ceramic and earthwork construction chronology developed for Triunfo and Versalles, and compared with existing regional archaeology and palaeoclimatology data. For the full 11,000 year palaeoecological record see Fig. 3 SOM and 4 SOM.

The Ceramic Chronology of Laguna Versalles

Three ceramic phases are defined from preliminary analysis of the limited ceramic material recovered from the excavations: Chocolatal (before 2400 to 1600 cal yr BP), Early Versalles (~1100-800 cal yr BP) and Late Versalles (800-300 cal yr BP; Fig. 1

SOM). The phases are recognizable by morphological and decorative attributes, but not paste, which generally contains ground ceramic (chamote), ground quartz, cauixi (freshwater sponge), and mica in a variety of combinations. The surfaces are eroded, but where preserved, are well smoothed and in some cases burnished. In a few fragments, red and brown slip is present. Preliminary dating for the chronological boundaries for these phases is based on 15 new AMS radiocarbon dates (SOM Table 4), however as the site was only partially excavated, it is possible that these chronological boundaries will change after future excavations.

The Pre-Ceramic Occupation prior to ADE Soil Formation (Before 4500 cal yr BP)

Before 4500 cal yr BP the sedimentation rate at LV is slow (<0.003 mm yr-1) indicating minimal erosion and a low energy depositional environment. Rainforest vegetation is present throughout the duration of the record, indicated by >40% Moraceae/Urticaceae pollen in the record. The presence of <1% of *Anadenanthera* (Fig. 3 SOM), a key indicator of modern SDTF, provides evidence that some component of SDTF was present around the lake at this time as these large and heavy pollen grains are most likely deposited near the parent tree and unlikely derived from long-distance transport. Maize pollen is present after ~5700 cal yr BP along with onset of low levels of fire activity and is consistent with low levels of regional human activity indicated by the SPD and site frequency data (Fig. 2G). Regional climate data from Pumacocha indicate climate conditions drier than present from 6000 to 5000 cal yr BP and becoming progressively wetter after ~4500 cal yr BP (Fig. 2H). Drier conditions likely promoted lower lake levels, which in turn supported high concentrations of the emergent macrophyte *Isoetes* (>60%, Fig. 3 SOM). Regional climate gets progressively wetter after ~5000 cal

yr BP, synchronous with a decline in *Isoetes* and increase in *Sagittaria* and Cyperaceae that may have outcompeted *Isoetes* for space in the shallow, eutrophic lake margins. Biomass burning and fire frequency (inferred from charcoal influx values) increase after ~4500 cal yr BP, reaching record levels ~2800 cal yr BP.

The Chocolatal Ceramic Phase and ADE Formation (Before 2400-1600 cal yr BP)

Sediment accumulation begins to increase (~ 0.007 mm yr-1) between 3000 to 2400 cal yr BP (Fig. 2D) coupled with an increase in fire activity ~2800 cal yr BP (Fig. 2F), a four-fold increase in total pollen accumulation (PAR), and 8% decline in trees and shrubs, a ~3% increase in palm pollen (Mauritia/Mauritiella, Euterpe, and Oenocarpus), a 18% increase in Mauritia/Mauritiella pollen accumulation, and the continued presence of maize pollen, (Fig. 2E, Fig. 3 SOM). Phytolith data from the archaeological soil profiles indicate the presence of manioc and leren (Calathea sp.) crops (Fig. 2C). Burning is indicated by soil macrocharcoal (particles/cm³) found after ~2400 cal yr BP, prior to the formation of anthropic soils and present throughout the soil profiles once the ADE/ABE soils form (Fig. 2B, Fig. 5-8 SOM). ADE/ABE soil formation begins ~2300 cal yr BP during the Chocolatal ceramic phase (Fig. 2A, Fig. 1 SOM, SOM Section 1. Triunfo Ceramics). The highest recorded sediment accumulation at LV occurs between ~1700 to 1100 cal yr BP (~0.017 mm yr⁻¹; Fig. 2D) coupled with an increase in biomass burning (Fig. 2F), decrease in both total PAR and Mauritia/Mauritiella PAR values, a ~20% decline in trees and shrubs, the continued presence of maize and sweet potato (*Ipomoea* sp.) pollen, and > 10% increase in palms (Mauritia/Mauritiella, Attalea, Euterpe, and Oenocarpus, Fig. 2E, Fig. 3 SOM). This period corresponds with increased regional human activity indicated by the increase in SPD and site frequency values after ~2400

cal yr BP (Fig. 2G), and the onset of slightly wetter, more variable precipitation conditions indicated by the δ^{18} O values from Pumacocha (Fig. 2H).

Early Versalles Phase (1100-800 cal yr BP)

After 1100 cal yr BP sedimentation decreases to (~0.008 mm yr-1) (Fig. 2D), synchronous with a decline in burning and maize pollen was only recorded in 1 sample from LV ~920 cal yr BP (Fig. 2F, 2E, Fig. 3 SOM). Tree, shrub, and palm pollen are stable through this period (Fig. 2E). There is a 20% increase in herb phytoliths at the expense of trees and shrubs in the ADE soil profiles, however change in vegetation composition is not large enough to be detected in the sediment accumulation rates or pollen data at LV (Fig. 2C). Increased biomass burning associated with crop cultivation is indicated by increased macrocharcoal in the soil profiles and the continued presence of manioc, maize, and leren phytoliths in both the ADE/ABE soils (Fig. 2C). The increase in forest clearance associated with the Early Versalles ceramic phase (~1100 to 800 cal yr BP) (Fig. 2A, Fig. 1 SOM, SOM. Section 1.Triunfo Ceramics) corresponds to an increase in regional human activity indicated by the SPD and site frequency values (Fig. 2G). Palaeoclimate exhibits drier conditions during this period associated with the MCA (1300-900 cal yr BP, Fig. 2H).

The Late Versalles and Ring Ditch Phase (800-300 BP)

After 800 cal yr BP, sediment accumulation remains stable (~0.008 mm yr-1, Fig. 2D) in the upper portion of the lake record accompanied by low levels of biomass burning with maize pollen only present in one sample (ca. 180 cal yr BP, Fig. 2E). In the ADE/ABE soil profiles, there is an increase in biomass burning and forest clearance associated with

increased soil macrocharcoal (particles/cm3; Fig. 2C, Fig. 5-8 SOM), declines in arboreal phytoliths, and increase in the proportion of herb phytoliths. Maize, manioc, and leren phytoliths indicate continued crop cultivation at the site (Fig. 2C, Fig. 5-8 SOM). This intensification of ADE land use is associated with the Late Versalles ceramic phase (~800 to 300 cal yr BP) (Fig. 2A, Fig. 1 SOM, SOM. Section 1.Triunfo Ceramics), the construction of earthwork architecture at the site including a site boundary zanja and an elliptical double ring ditch [76]. The development of these earthworks is associated with increased regional human activity and earthwork construction, and increased SPD and site frequency values (Fig. 2G). During the later portion of the Late Versalles phase, regional palaeoclimate becomes progressively wetter (700 to 200 cal yr BP) associated with the LIA period and increased monsoon intensity in the region [71,72] (Fig. 2H).

Discussion

Versalles in a Regional Palaeoecological Context

Through the early and mid-Holocene, the presence of components of SDTF around LV is indicated by a key dry forest taxa *Anadenanthera* [97,98] (Fig. 3 SOM). High concentrations of *Isoetes* indicate lower lake levels [99] which is consistent with regional lake records that track drier conditions associated with the mid-Holocene Dry Event (MHDE) [100–104], including Laguna Bella Vista and Laguna Chaplin [10,105,106], Cuatro Vientos [107], Laguna Oricore [17,62], Lakes Chalalán and Santa Rosa [20], and Lake Rogaguado [108]. However, despite the presence of this key SDTF taxa at LV, the presence of >40% Moraceae/Urticaceae and <20% Poaceae pollen throughout the Holocene indicate a greater abundance of TFRF vegetation compared with existing regional lake records [10,17,105–109]. These regional lakes were dominated by SDTF,

savannahs, and gallery forest patches until the late Holocene when these records document a distinct increase in TFRF vegetation associated with the expansion of the humid rainforest and southward migration of the savannah-rainforest ecotone to its most southern extent in the last 50,000 years [10,17,105,106,109]. Despite being along the ARE boundary, the continued dominance of TFRF at LV suggests a stable rainforest ecosystem throughout the Holocene (SOM Fig. 3-4 SOM). Furthermore, it is likely that the northernmost extension of the savannah boundary associated with the last Glacial period does not reach LV. The presence of human occupation at LV after 5700 cal yr BP is consistent with an increasing body of evidence suggesting that the earliest settlers of the Amazon preferred vegetation mosaics and productive ecotones [5]. This included palm-dominated tropical forests-savannah-riverine mosaics, such as LV, where early occupants could exploit a range of vegetation types and resources.

Pre-ADE Maize Cultivation and Cultural Burning

The paired archaeological and palaeoecological reconstructions at LV, combined with regional archaeological histories, offer a unique opportunity to explore the influence of human-environment interactions in the ARE. Low level fire activity is present at LV throughout the record and begins to increase after 4500 cal yr BP. Drought conditions are a key factor in increased forest flammability in modern Amazon vegetation [110,111]. The natural occurrence of fire is low in rainforest systems as a result of the high fuel moisture [112]. As a result of the low incidence of natural fire, the occurrence of fire in rainforest systems has previously been interpreted as human-caused fire activity [61,113]. Thus, if drought was the dominant driver of fire at LV, the highest fire activity would be associated with the driest climate conditions ~6000-5000 cal yr BP (Fig. 2F) [70].

Fire activity at LV increases slightly ~6000 cal yr BP a few hundred years prior to the first evidence of maize pollen (Fig. 2E, Fig. 3 SOM), a pattern common in other Amazon lakes [17,20,113–115]. There is a more substantial increase in fire activity and fire frequency after 4500 cal yr BP, associated with the presence of maize pollen, increased regional human activity, and a progressive shift towards wetter regional climate conditions (Fig. 2H). The presence of maize pollen in the palaeorecord is interpreted to indicate cultivation on or near the lake shore as a result of its large pollen size and minimal dispersal range [80]. Thus, the synchronous onset of fire activity combined with the presence of maize pollen suggests intentional cultural burning was the dominant driver of fire at LV. The early occupants at LV likely used fire for local forest clearance in order to utilize the nutrient rich soils around the lake shore for maize cultivation (Fig. 3). This interpretation is consistent with extensive ethnographic and archaeological evidence documenting the use of low severity burning as a tool to clear land for crop cultivation and to increase soil fertility for nutrient-demanding crops such as maize [116–118].

The occurrence of maize pollen at LV after ~5700 cal yr BP is consistent with a temporal gradient of maize dispersal that begins outside Amazonia and reaches the ARE after 7000 cal yr BP [65,108,114,119–121]. Earliest maize in the region appears ~6850 cal yr BP in anthropic forest islands of the seasonally flooded savannahs to the SW of Triunfo [3], Lake Rogaguado ~6500 cal yr BP [108], and in the nearby Monte Castelo shell-mound ~5300 cal yr BP [4,122].

Polyculture Agroforestry and ADE/ABE Formation

Regional land use intensification begins after ~2800 cal yr BP associated with a progressive increase in erosion (indicated by increased sediment accumulation rates),

increased forest clearance (indicated by a 20% decrease in trees and shrubs), the presence of polyculture agroforestry [5,65] (indicated by a 10% increase in edible palms including *Mauritia/Mauritiella*, *Attalea*, *Euterpe*, and *Oenocarpus* and the cultivation of multiple crops including maize, manioc, sweet potato, leren), and record levels of cultural burning. Increased fire activity ~2800 cal yr BP does not correspond to regional drying conditions suggesting that cultural burning, as opposed to drought, continues to be the dominant driver of fire at this time.

The increase in land clearance caused by cultural burning, likely represents the antecedent conditions for the establishment of polyculture agroforestry [65], which is later followed by ADE/ABE soil formation at LV (~2400 cal yr BP). The use of cultural burning and crop cultivation prior to the development of ADE/ABE soils is similar to land use practices documented elsewhere in the Amazon [61,62,65,113]. The presence of maize and manioc intercropping [118,123–126], prior to the formation of ADE/ABE soils, is consistent with the hypothesis of prolonged landscape domestication characterized by progressive soil enrichment [118] through the addition of waste, refuse, and charcoal [127,128]. Similar to the hypothesis proposed by Arroyo-Kalin (2012), the early-mid Holocene tropical forest cultures around LV likely exploited refuse middens or small home gardens for polyculture crop cultivation prior to the development of ABE swiddens (~2400 cal yr BP) associated with polyculture cultivation around LV [76]. Additionally, our data support previous interpretations that manioc was likely domesticated in home gardens and only later expanded away from settlements with the increase in population and development of larger ABE swiddens to increase food production [42].

After the formation of the ADE/ABE soils at LV, there is a peak in land use intensification, indicated by record level erosion, peak forest clearance both locally,

(indicated by a 20% increase in herb phytoliths) and regionally (indicated by a 30% decrease in trees and shrubs), coupled with a 13% increase in edible palms, along with maize, sweet potato, manioc and leren cultivation. These data indicate a combination of polyculture agroforestry and forest clearance at this time (Fig. 2B-F, Fig. 3). This land use intensification occurs during the transition between the Chocolatal and Early Versalles ceramic phases (~1600 to 1300 cal yr BP) (Fig. 2A, Fig. 1 SOM, SOM. Section 1.Triunfo Ceramics) and corresponds to a decrease in regional human activity indicated by lower SPD and site frequency values (Fig. 2G). The cultural transformation associated with the decrease in regional human activity and the distinct transition from Chocolatal to Early Versalles cultural phases is associated with renewed vigor in land clearance that may indicate the arrival of a new population to LV at this time. This cultural transition may be associated with the transcontinental migration of the forest-dependent Tupi-Guarani culture from southern Amazonia to southern Brazil ca. 2000-3000 cal yr BP [107,129,130].

The exploitation of a diverse range of cultivated, managed and potentially wild species is similar to subsistence strategies documented for the last 6000 years at the nearby site of Monte Castello (MC, ~40 km away) [4,122]. At MC, there is progressive land use diversification, rather than intensification through the Holocene [122]. However at LV, the increase in land clearance, erosion, cultural burning, polycrop cultivation, and the later formation of ADE soils associated with domestic spheres and ABE soils associated with crop cultivation [76], suggest land use practices were both diversifying and intensifying during the late Holocene.

The diverse and intensive land use strategy employed at LV persisted through significant cultural reorganization indicated by the transitions in the ceramic chronologies

and later fortification (Fig. 3). LV fits into a broader context of cultural transformation along the ARE and pan-Amazonian evidence of fortification during this period [26,27,29,31,131,132]. Coupled with significant climate variability associated with the MCA and LIA [71,133,134], intensive polyculture agroforestry and cultural burning persisted (indicated by the continued enrichment in edible palm species and poly-crop cultivation). ARE land use is remarkably similar to polyculture agroforestry land use strategies employed elsewhere in the Amazon interior, despite the different ecological settings and cultural histories across the Amazon [5,135–137], suggesting stability in this land use system.

Furthermore, the continued presence of maize pollen until ~180 cal yr BP and maize and manioc phytoliths after ~140 cal yr BP (Fig. 2C, 2E) suggests that this area of the ARE did not experience immediate depopulation following the arrival of European settlers and that Indigenous populations did not abandon polyculture at LV following European contact (ca. 1541 in Amazonia). This interpretation is supported by corroborating evidence of (i) occupation following contact at Laguna Chaplin [10], Laguna San Jose [138] and Laguna El Cerrito [139], (ii) extensive archaeological evidence in the Bolivian lowlands [62,140,141] and (iii) European chronicles from the seventeenth century. In particular, Father Eder [142] and other chronicles [143] described sizeable populations living in large, well-planned fortified settlements and cultivating maize as one of the important crops.

Forest Composition, Structure, and Cultural Burning in the ARE

Our data suggest ~5700 years of Indigenous cultural burning influenced forest composition and structure. Palms, such as *M. flexuosa*, are not traditionally considered

fire tolerant given their adaptation to humid soils along lake and stream margins [144]. However, in a recent study on the impact of fire in the stand structure of *M. flexuosa,* canopy structure in fire-impacted margins was significantly more open and was coupled with significantly higher reproductive output, producing up to three times as many individual fruit as their non-fire impacted counterparts [54]. These data demonstrate that *M. flexuosa* stands have sufficient plasticity in reproductive output to sustain viable populations across a range of fire regimes [54]. The correlation with *M. flexuosa* PAR and charcoal influx and fire frequency values (Fig.2E-F) suggest that the use of frequent cultural burning associated with polyculture agroforestry, likely created more open canopy structure and influenced forest composition by increasing post-fire reproductive output of these economically important palms.

Similar to *M. flexuosa*, fire stimulates post-fire regenerative and reproductive growth of *Attalea*, which has the capacity to survive human-induced stress including cutting and burning as a result of cryptogeal germination of the apical meristem in the ground [145]. Ethnographic evidence from Amazonian Kayapo Indigenous groups documents intentional management of the composition of secondary forest regrowth in areas cleared for polyculture agroforestry, purposefully planting groves of *Attalea* and other long-lived trees [60,145,146]. Previous research has proposed that the increase in palm-dominated stands of palms such as *Attalea*, are an artifact of land use practices following the European encounter, including cattle ranching and large development projects [147]. Alternatively, other researchers have argued that *Attalea* is an indicator of human land use in pre-Columbian times [55,148]. The increase in *Attalea* pollen after ~2000 cal yr BP at LV suggests palm dominated stands originate during the cultural transition between the Chocolatal and Early Versalles phase associated with the

Indigenous cultural burning and polyculture agroforestry, ~1000 years prior to European conquest.

The use of fire to influence the composition and structure of the ecotonal boundary of the ARE has also been documented at Laguna Oricore and Laguna Granja (ca. 75 km SW of Versalles). Fire was used to keep landscapes open against the backdrop of the southward migration of the rainforest boundary [17]. At LV however, evidence of the persistence of the rainforest system is inferred from the continued presence of arboreal pollen and phytoliths from the local (soil cores) and regional (lake) scale. Despite significant climate variability and intensive human activity that influenced forest composition and structure, the rainforest ecosystems around LV maintained their integrity along this ecotonal boundary during the Holocene.

Legacy of Humans in the ARE and Modern Management Implications

The data from LV suggest polyculture agroforestry and cultural burning was a stable land use system [149] that persisted through marked climate variability (i.e. the MHDE, MCA, LIA) and social change. However, this land use strategy did not alter the stability of the ARE rainforest at LV, as indicated by the continued presence of > 40% rainforest pollen throughout the record, despite the continued enrichment in palms after ~2000 cal yr BP. Remote sensing data from Iténez Forest Reserve [76] demonstrate that modern ADE forests have lower canopy moisture and increased drought susceptibility [150], thus making them more fire prone. Recent research suggests that millennia of fire activity in forests in the south-western Amazon may have precondition forests to be more resilient to the threat of increased modern fire activity opposed to other regions in the Amazon (e.g. the north and northwestern Amazon) [14]. At present, the anthropogenic

forests of the Bolivian ARE remain protected as a national reserve and are stable under current disturbance and climate regimes. Recent modelling studies suggest that while human land use intensification poses a greater threat to increased fire activity than drought [12], the compounding influences of climate change, deforestation and reduced evapotranspiration, coupled with increased human-caused ignitions will likely pose an increasing threat to the stability of the ARE in the upcoming century [13].

Summary

The data from LV indicate both a stable rainforest ecosystem and stable land use system along the ARE since the mid-Holocene against a backdrop of variable climate and cultural transformations. Despite being close to the ecotone boundary, LV was forested throughout the Holocene, suggesting that the northernmost extension of the savannah boundary associated with the last Glacial Period did not reach LV. Polyculture agroforestry and cultural burning persisted within this system for millennia resulting in altered vegetation composition and structure that is still detectable using modern remote sensing data. While the ARE is stable under current disturbance regimes, it is likely that the ARE will be increasingly susceptible to the compounding factors of climate change and human land use intensification that are projected to increase fire activity in the ARE region in the upcoming century.

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Data Accessibility

Supplementary data to this article can be found online at Zenodo open source repository at https://doi.org/XXX once these data are published.

Author Statement

SYM, JI, SE, MR, DA, JGS and DU designed the research; JI, SE, SYM, MR, DA, LH, CB, JGS, carried out the archaeological, archaeobotanical and palaeoecological work; SYM led the writing of the paper with contributions from all other authors.

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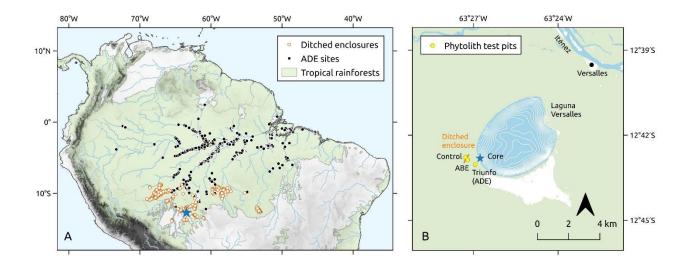
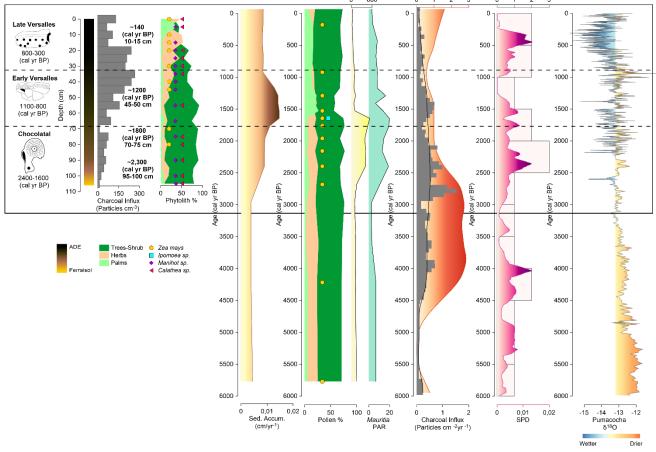


Figure 1 Regional Study Map Laguna Versalles. A: regional location of Laguna Versailles and other ADE sites in Amazonia. B: bathymetry of Laguna Versalles ranging from 1 to 2.8 m depth (core depth 2.2 m), location of Versalles village (black dot), lake sediment core (blue star), Triunfo excavation site and ditch enclosure identified in the field, and ADE: Amazonian Dark Earths, ABE: Amazonian Brown Earths, and control soil profiles (yellow circles).



A. Local Archaeology B. Local Fire C. Local Vegetation D. Erosion E. Regional Vegetation F. Regional Fire G. Regional Archaeology H. Palaeoclimate Total PAR 0 600 0 1 2 3 0 1 2 3

Figure 2: Laguna Versalles Data Summary. A. Local Archaeology summarizing the ceramic phases and ADE soil profile, B. Local Fire based on soil charcoal (grey), C. Local Vegetation and crops identified based on phytolith data, D. Erosion based on sediment accumulation from Laguna Versalles, E. Regional Vegetation based on pollen data grouped into trees-shrubs, herbs, palms, and crop pollen identified, Total Pollen Accumulation (PAR; yellow) and *Mauritia* PAR (light blue), F. Regional Fire based on lake sediment charcoal influx (grey) and CHAR Analysis [92] including background (black line) and fire frequency (orange fill), G. Regional Archaeology based on SPD values calculated from 39 AMS dated archaeological sites (SOM Table 3-4) and number of archaeological sites per 500 year smoothing window (pink bars), H. Regional Palaeoclimate based on δ^{18} O from Pumacocha [70].



Figure 3 Conceptual figure of changing Indigenous land use and cultural burning at Laguna Versalles: including early maize cultivation and cultural burning, polyculture agroforestry and ADE soil formation, cultural burning and palm enrichment, and ring ditch construction.

Supplemental Information

SOM Table 1: Modern botanical survey of vegetation around Laguna Versalles.

Family Fabaceae	Common Name Cari cari lenticelado	Scientific Name Albizia cf.subdimidiata
Rubiaceae	Rubiaceae	Amaioua guianensis
Annonaceae	Chirimoya 2	Anaxagorea dolichocarpa
Lauraceae	Canelón	Aniba panurensis
Arecaceae	Chonta	Astrocaryum sp.
Arecaceae	Cusi macho	Attalea maripa
Arecaceae	Motacú	Attalea phalerata
Moraceae	Murure 2	Batocarpus amazonicus
Moraceae	Mururé	Brosimum utile
Myrisiticaceae	Cundarú	Calypthranthes lucida
Annonaceae Cannabaceae	Chirimoya silvestre Cusé	Cardiopetalum calophyllum Casearia decandra
Cannabaceae	Fariña seca	Celtis schippii
Annonaceae	Chirimoya silvestre	Crematosperma leiophyllum
Araliaceae	Blanquillo	Dendropanax arboreus
Sapotaceae	Leche leche	Ecclinusa cf. ramiflora
Sapotaceae		<i>Ecclinusa</i> sp.
Arecaceae	Asaí	Euterpe precatoria
Apocynaceae	Pancho amarillo	Geissospermum reticulatum
Arecaceae	Jatata	Geonoma deversa
Olacaceae	Itaúba barcina	Heisteria cf. spruceana

Fabaceae	Pacay	Inga acreana
		0
Fabaceae	Pacay tutado	Inga cf. alba
Fabaceae	Pacay	<i>Inga</i> sp.
Myrisiticaceae	Sangrón	Iryanthera juruensis
Euphorbiaceae	Mabea	Mabea fistulifera
Fabaceae	Cuadrado	Machaerium sp.
Moraceae	Mora	Maclura tinctoria
Lauraceae	Itaúba amarilla	Mezilaurus itauba
Melastomataceae	Miconia común	Miconia poeppigii
Melastomataceae	Palo fierro	Mouriri myrtifolia
Lauraceae	Canilla de paico o de camba	Nectandra cuspidata
Fabaceae	Desco	Ormosia sp.
Fabaceae	Cari cari espinudo	Parapiptadenia pterosperma
Fabaceae	Toco macho	Parkia pendula
Strelitziaceae	Patujú gigante	Phenakospermum guianensis
Lythraceae	Coloradillo	Physocalymma scaberrimum
Euphorbiaceae	Algodonillo	<i>Plukenetia</i> sp.
Fabaceae	Cari cari de altura	Poeppigia procera
Urticaceae	Ambaibo	Pourouma cf. guianensis
Moraceae	Nuy	Pseudolmedia laevis
Rubiaceae	Cafecillo	Psychotria borgensis
Rhamnaceae	Turere	Rhamnidium elaeocarpum
Fabaceae	Penoco	Samanea tubulosa
Euphorbiaceae	Peloto	Sapium cf. haematospermum
Euphorbiaceae	Peloto	Sapium cf. pallidum
Araliaceae	Guitarrero	Schefflera morototoni
Elaeocarpaceae	Urucusillo	Sloanea sp.

Smilacaceae	Hojas con dos bandas	<i>Smilax</i> sp.
Arecaceae	Pachiuva sin petaca	Socratea exhorriza
Moraceae	Moraceae aserrada	Sorocea guilleminiana
Anacardiaceae	Cedrillo	Spondias mombin
Fabaceae	Maní	Sweetia fruticosa
Fabaceae	Palo Santo	Tachigali bracteosa
Malvaceae	Mazorquilla	Theobroma speciosum
Clusiaceae	Achachairú	<i>Tovomita</i> sp.
Burseraceae	Ocre	Tratinickia boliviana
Urticaceae	Pica pica	Urera cf. caracasana
Myrisiticaceae	Palo colorado fisurado	Virola pavonis
Myrisiticaceae	Raya roja sangre	Virola surinamensis
Annonaceae	Piraquina garronuda	Xylopia benthamii
Annonaceae	Envira colorada	<i>Xylopia</i> sp.
Rutaceae	Saúco	Zanthoxylum sp.

Site	Depth (cm)	Lab #	Age BP	δ ¹³ C	Cal BP 2σ
Laguna Versalles	10	491623	1260 ± 30	-23.3	1186 - 1061
Laguna Versalles	20	491624	1840 ± 30	-24.2	1825 - 1694
Laguna Versalles	28	491625	2560 ± 30	-22.1	2745 - 2485
Laguna Versalles	35	491626	4040 ± 30	-20.6	4573 - 4406
Laguna Versalles	42	491627	9910 ± 30	-23.2	11363 - 11202

SOM Table 2: AMS Radiocarbon Dates Laguna Versalles sediment core

Site	Code	¹⁴ CAge	¹⁴ C SD	Lab#	Tradition	Reference
Monte Castelo	RO-PN-08	3945	110	SI-6845	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	3920	85	SI-6847	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	3700	30	Beta-408413	Bacabal	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	3580	105	SI-6846	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	3160	70	Beta-66309	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	2760	100	Beta-66308	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	2475	105	SI-6843	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	2270	105	SI-6844	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	2060	60	Beta-106286	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	1970	80	Beta-103184	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	1540	80	Beta-106285	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	810	70	Beta-103185	Bacabal	Miller 2009
Monte Castelo	RO-PN-08	4350	130	Beta-103186	Sinimbu	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	4300	80	SI-6855	Sinimbu	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	4455	100	SI-6852	Unclassified	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	4395	70	SI-6848	Unclassified	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	8350	70	Beta-103187	Cupim	Miller 2009
Monte Castelo	RO-PN-08	7010	80	Beta-118274	Cupim	Miller 2009
Monte Castelo	RO-PN-08	6316	105	SI-6850	Cupim	Miller 2009
Monte Castelo	RO-PN-08	5970	80	Beta-118275	Cupim	Miller 2009
Monte Castelo	RO-PN-08	5605	95	SI-6853	Cupim	Miller 2009
Monte Castelo	RO-PN-08	5140	23	CEZ-32117	Cupim	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	5159	33	CEZ-32116	Sinimbu	Pugliese Jr. 2018
Monte Castelo	RO-PN-08	5165	80	SI-6854	Sinimbu	Miller 2009
Monte Castelo	RO-PN-08	5065	85	SI-6849	Sinimbu	Miller 2009
Monte Castelo	RO-PN-08	4810	90	Beta-66310	Sinimbu	Miller 2009
Monte Castelo	RO-PN-08	4570	30	Beta-408414	Sinimbu	Pugliese Jr. 2018
RO-PN-13	RO-PN-13	3935	105	SI-6851	Bacabal	Miller 2009
Triunfo		2270	30	Beta-488190	Chocolatal	This study
Triunfo		1840	30	Beta-488189	Chocolatal	This study
Triunfo		1670	30	Beta-488187	Chocolatal	This study
Triunfo		400	30	Beta-488185	Versalles	This study
Triunfo		320	30	Beta-488186	Versalles	This study
Versalles		2380	30	Beta-488182	Chocolatal	This study
Versalles		1000	30	Beta-488180	Versalles	This study
Versalles		660	30	Beta-488184	Versalles	This study
Versalles		390	30	Beta-488179	Versalles	This study
Versalles		260	30	Beta-488183	Versalles	This study

SOM Table 3: AMS Radiocarbon dates used in SPD Analysis.

SOM Table 4: AMS Radiocarbon Dates Triunfo Archaeological Site. Cal BP 2σ calculated using Calib [151].

Site	Excavation	Context	Lab #	Age BP	δ13C ‰	Cal BP 2σ
Versalles	T10	F2	488179	390 ± 30	-26.5	426-507
Versalles	T10	F9	488180	1000 ± 30	-26.4	900-957
Versalles	T62	Ceramic Cache	488182	2380 ± 30	-26.7	2342-2491
Versalles	ZT1	2nd Construction	488183	260 ± 30	-26.2	278-330
Versalles	ZT1	1st Construction	488184	660 ± 30	-22.7	625-671
Triunfo	Ring Village	1st Construction	488185	400 ± 30	-26.7	428-512
Triunfo	Inner Ditch	Base of ditch	488186	320 ± 30	-24.7	306-463
Triunfo	Chocolatal	C3	488187	1670 ± 30	-27.8	1515-1621
Triunfo	Chocolatal	C8	488189	1840 ± 30	-26.2	1699-1826
Triunfo	Control pit	75 cm	494922	2120 ± 30	-23.5	1998-2150
Triunfo	ABE	75 cm	494921	3220 ± 30	-20.5	3375-3481
Triunfo	ADE	95-100 cm	488190	2270 ± 30	-23.7	2156-2255
Triunfo	ADE	70-75 cm	494920	1820 ± 30	-23.1	1694-1798
Triunfo	ADE	45-50 cm	494919	1280 ± 30	-23.9	1175-1288
Triunfo	ADE	10-15 cm	500929	140 ± 30	-25.7	182-279

Supplemental Figures

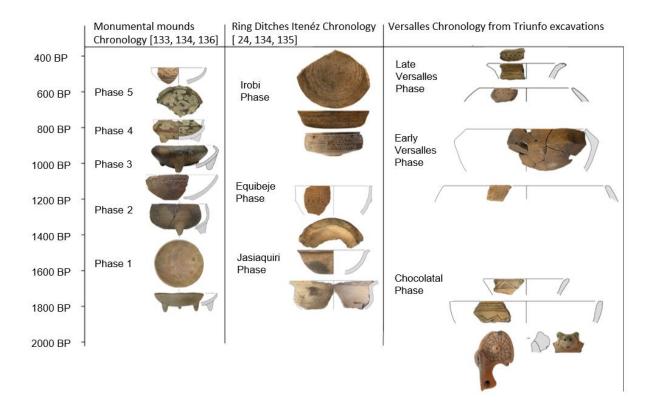


Fig. SOM1 Ceramic Chronology for Triunfo Archaeological Site compared with existing ceramic chronologies for the region [30,152–155].

A. Summary of the Versalles ceramic chronology

The Chocolatal Phase (400 BC-400AD/2400-1600 cal yr BP)

The Chocolatal phase (Fig.1 SOM) is characterized by open bowls with straight walls and direct edges. In some cases, the lips are flattened or beveled and have incised or fine dotted lines. The external decoration is incised with reticulated triangles. This same decoration also appears on the necks of open globular vessels or closed globular pots. Cooking pots have open, thickened edges and flat bases. Another important characteristic of this phase is the presence of zoomorphic decoration (e.g. parrots and

bats). The presence of some pedestal bases and some bowls with open edges with internal decoration. are proof of the contemporary relationship with the Jasiaquiri phase.

Early Versalles (900 - 1200 AD/1100-800 BP)

Closed spheroidal bowls with simple rims and rounded lips are very common (Fig. 1 SOM). Open vessels and those with straight walls are also present. Most vessels are decorated with incised concentric staggered motifs on the outer surface. which is the most diagnostic characteristic of this phase. Vertical incised lines near the vessel rim. and a line of dots or circular impressions on the lips are also common decorations. The commissure on the lips appears only in association with this ceramic phase.

Late Versalles (1200 - 1700 AD/800-300 BP)

The most common shapes in the Versalles Tardío phase are open vessels with straight walls and thickened or coiled rims (Fig. 1 SOM). The primary decorative characteristic is two lines of dots on the lip or around the rim of the vessel. This decoration is also present on the rim of globular pots with open necks. The fairing bowls have a band applied with elongated dots on the apex of the vessel or on the fairing.

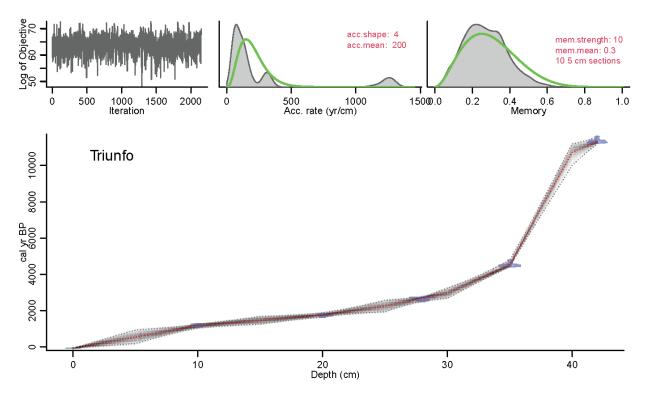


Figure 2 SOM: Laguna Versalles Age-Model. Age-depth model with MCMC iterations (top left) and priors (green curves) and posteriors (grey histograms) for accumulation rate (top middle) and memory (top right). The age model iterations (black hatching) are based on radiocarbon ages (blue pdfs), with model mean (red dashed) and 2s (black dashed) distributions.

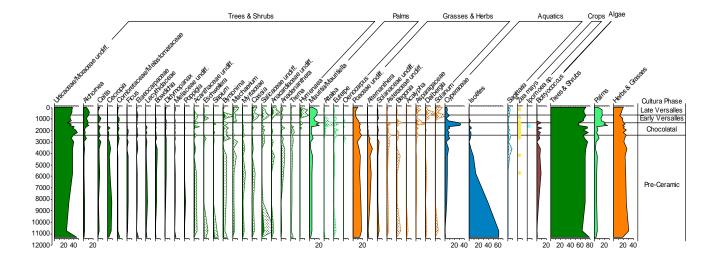


Figure 3 SOM: Laguna Versalles Pollen Data. Percentage pollen diagram (dotted silhouettes show 10X exaggeration curves); Dark green represents trees and shrubs, light green represents palms, orange represents herbs, dark blue indicated aquatics, symbols represent total counts of crop pollen: yellow circle maize (*Zea mays*), blue square sweet potato (*Ipomoea*). Cultural phases grouped by ceramic traditions.

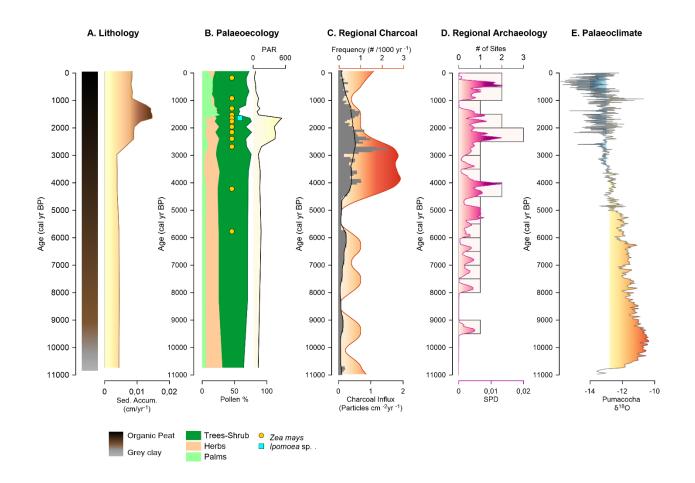


Figure 4 SOM: Laguna Versalles Data summary for the last 11,000 years. A. Sediment lithology and sediment accumulation rate (cm/yr⁻¹), B. Regional Vegetation based on pollen data grouped into trees-shrubs, herbs, palms, and crop pollen identified, Total Pollen Accumulation (PAR; yellow), F. Regional Fire based on lake sediment charcoal influx (grey) and CHAR Analysis [92] including background (black line) and fire frequency (orange fill), G. Regional Archaeology based on SPD values calculated from 39 AMS dated archaeological sites (SOM Table 3) and number of archaeological sites per 500 year smoothing window (pink bars), H. Regional Palaeoclimate based on δ^{18} O from Pumacocha [70].

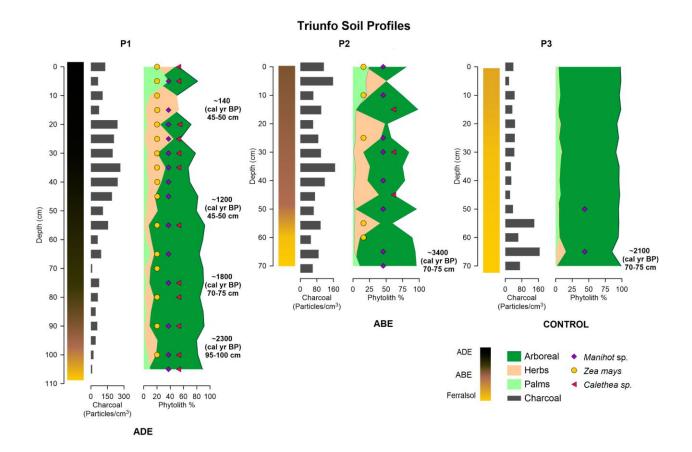


Figure 5 SOM: Phytolith summary profiles from Triunfo excavations from the Amazonian Dark Earth (ADE), Amazonian Brown Earth (ABE), and Control soil profiles. Vegetation grouped into arboreal (dark green), herbs (orange), and lights green (palms). Crops indicated by symbols: *Zea mays* (yellow circle), *Manihot* sp. (purple diamond), and *Calethea* sp. (pink triangle).

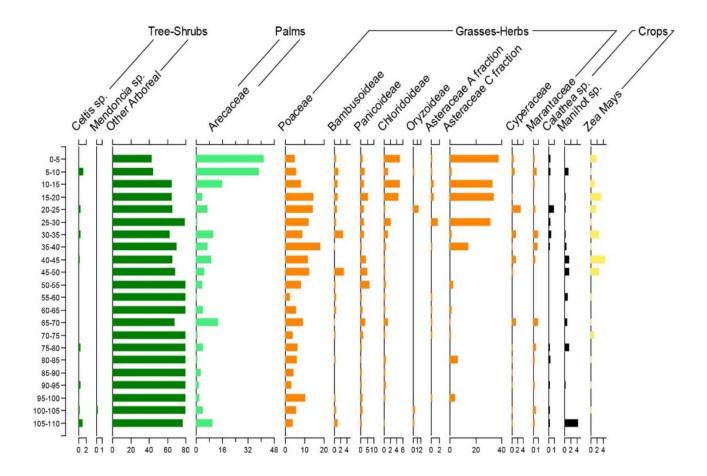


Figure 6 SOM Amazonian Dark Earth phytolith profile. Phytoliths grouped into arboreal (dark green), palms (light green), and herbs (orange). Number of *Zea mays, Manihot* sp., and *Calathea* sp. crop phytoliths plotted to the right of the graph.

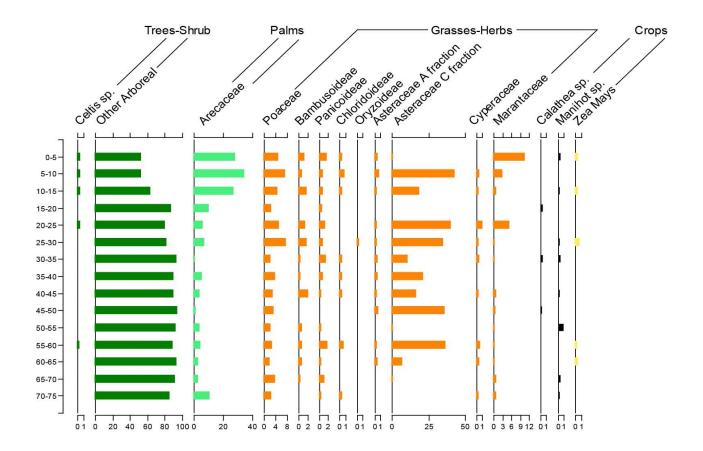


Figure 7 SOM Amazonian Brown Earth phytolith profile. Phytoliths grouped into arboreal (dark green), palms (light green), and herbs (orange). Number of *Zea mays, Manihot* sp., and *Calathea* sp. crop phytoliths plotted to the right of the graph.

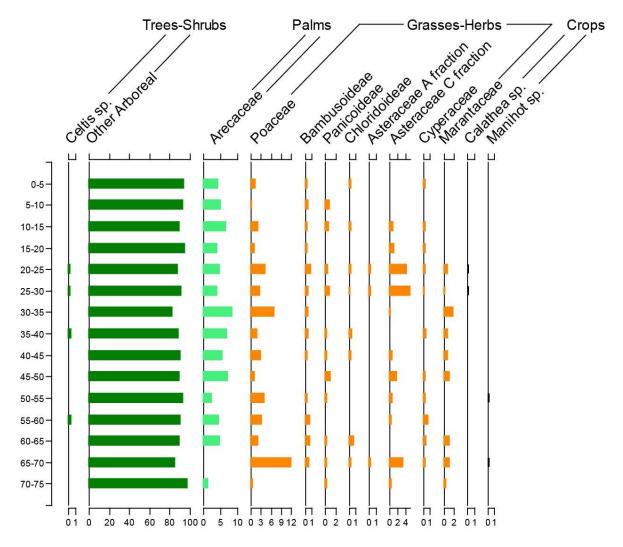


Figure 8 SOM Control phytolith profile. Phytoliths grouped into arboreal (dark green), palms (light green), and herbs (orange). Number of *Manihot* sp., and *Calathea* sp. crop phytoliths plotted to the right of the graph.

Supplemental Online Material References

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