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

S. Yoshi Maezumi[1]*, Sarah Elliott[2], Mark Robinson[3], Carla Jaimes Betancourt[4], Jonas Gregorio de Souza[5], Daiana Alves[6], Mark Grosvenor[7], Lautaro Hilbert[8], Dunia H. Urrego[9], William D. Gosling[1], José Iriarte[3]

[1]*Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity & Ecosystem Dynamics, University of Amsterdam, The Netherlands 1090 N, *s.y.maezumi@uva.nl (Corresponding author), W.D.Gosling@uva.nl*

[2]*Department of Archaeology and Anthropology, Bournemouth University. Talbot Campus, Fern Barrow, Poole, BH12 5BB, UK. selliott@bournemouth.ac.uk*

[3]*Department of Archaeology, University of Exeter, United Kingdom. markrobinson.uk@gmail.com , J.Iriarte@exeter.ac.uk*

[4]*Department for the Anthropology of the Americas, University of Bonn, Bonn, Germany. cjaimes@uni-bonn.de*

[5]*Department of Humanities, University Pompeu Fabra, Barcelona, Spain. jonas.gregorio@upf.edu*

[6]*Department of Anthropology, Federal University of Pará, Belém, Pará, Brazil. daianatalves@gmail.com*

[7]*Department of Geography, King's College London, London, UK. mark.grosvenor@kcl.ac.uk*

[8]*Laboratório de Arqueologia dos Trópicos, Museu de Arqueologia e Etnologia, Universidade de São Paulo, São Paulo, Brazil. lmaxhilbert@yahoo.com.br*

[9]*College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom. D.Urrego@exeter.ac.uk*

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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 of the ARE 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 cultivation 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 agroforestry indicated by increased edible palms, including: *Mauritia flexuosa* and *Attalea* sp. and record levels of burning suggesting fire played an important role in agroforestry practices. The frequent use of fire altered ADE/ABD forest composition and structure by controlling ignitions, decreasing fuel loads, and increasing the abundance of plants preferred by humans. Cultural burning and polyculture agroforestry provided 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 fire-adverse rainforest vegetation with infrequent incidence of fire and fire-adapted savannah vegetation with frequent fire occurrence [7,8]. Despite the prevalence of modern fire, 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 [23–25] and earthwork construction (after ~2500 cal yr BP) [26–31]. Cultural burning is one of the most powerful tools used by humans 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 and contributed to the formation of anthropogenically modified soils: Amazonian Dark Earth (ADE) and Amazonian Brown Earth (ABE) soils [42–44].

The frequent use of cultural burning associated with Indigenous polyculture and ADE/ABE formation [43,45] influenced key components of the palaeofire regime, such as fire severity, fire frequency, and fire intensity [46]. 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 [40,47]. 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 [48], in turn, increasing the abundance of fire tolerant plants while decreasing fire intolerant seed banks [49–59].

Persistent Indigenous legacies from cultural burning have been demonstrated elsewhere in Amazon rainforest ecosystems [16,20,60,61]; 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, human land use, and cultural burning on ARE ecosystems in the Bolivian Amazon, we implemented a multi-proxy approach [62–64] 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]. There is 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 [65–68]. The archaeological and palaeoecological data are compared with palaeoclimate data from Pumacocha (~1300 km west of LV) [69], 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) [70,71].

Materials and Methods

Study Site

We selected the Iténez Forest Reserve, a ~5000-km^2 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, inter-tropical humid with a wet season between November and March [72]. The mean annual rainfall is 1300 mm per year and the annual temperatures range between 23 °C and 27 °C [72]. The region is an ecological transition zone between *terra firme* (non-flooded) dense-canopy, humid evergreen rainforest floristically linked to the Madeira-Tapajos ecoregion [73,74], and the savannahs of the Beni Basin (135,000 km^2) 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 [65–68].

Research was conducted in and around Laguna Versalles (LV), a large (~21.6 km^2), 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-speaking Indigenous community, which is built atop a pre-Columbian Indigenous settlement [75]. 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 [75].

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 Herbario del Oriente Boliviano (USZ), Museo de Historia Natural Noel Kempff Mercado (Santa Cruz, Bolivia) 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 a depth of 2.2 m) (Fig. 1A-B). The maximum lake depth was 2.8 meters (Fig. 1B). 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 [76,77] 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 (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’ [78]. Dates were modelled using the IntCal20 Northern Hemisphere calibration curve [79]. The Northern versus Southern calibration curve [80] was selected 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 ^{14}C signal to the low-latitude Southern Hemisphere [81]. As LV is located in the low latitudes (12.7°S), 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 [82] in R [83–85]. 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 cm^3) was prepared using a standard digestion protocol [86] including an additional sieving stage to concentrate large cultigen pollen types, such as maize (*Zea mays*), manioc (*Manihot esculenta*) and sweet potato (*Ipomoea batatas*) [87]. 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 [77]. 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) [88]. 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: (i) 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, (ii) the co-occurrence of *Ipomoea* and maize pollen, and (iii) 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 [89]. Subsampled material (1 cm^3) 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 $cm^{-2}yr^{-1}$) 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 methodologies [90,91]. Charcoal peaks are interpreted as a fire episode and the time-difference between peaks reflects 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 [75]. Ceramic material was analyzed following standard procedures to assess changes in form, paste, and decoration, and compared to regional collections (Fig. 1SOM). Ceramic analysis consisted of observing the fresh fractures of 1044 ceramic fragments under binocular loupes (10 to 25x magnification). Groups of pastes were defined by comparison and a sample was selected for thin sections for compositional characterization and angularity by petrographic analysis with polarized light microscopy.

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 [75]. Archaeobotanical analysis of the samples (phytoliths and macrocharcoal) was conducted following standard procedures [64,75]. Full archaeobotanical analysis is presented elsewhere [5,75], with key results being discussed below.

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. These data are compared with published regional archaeology data summarized using Sum Probability Distributions (SPDs) [92] constructed from 150 regional radiocarbon dates from 39 archaeological sites in the Bolivian lowlands [10]. The SPD curve is plotted along with a histogram of the number of occupied archaeological sites based on the medians of the calibrated dates per 200-year intervals (Fig. 2H) [10]. Additionally, these data are compared with transitions in regional earthwork phases from the Southwestern Amazon and the Llanos de Moxos archaeological regions [93] (Fig. 2H). Palaeoclimatology data from Pumacocha [69] is used to contextualize regional changes in palaeohydrology. 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, not including 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 3), however as the site was only partially excavated, it is possible that these chronological boundaries may 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 seasonally dry tropical forest (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 (Fig. 2F) along with onset of low levels of fire activity (Fig. 2E) and is consistent with low levels of regional human activity indicated by the SPD and site frequency data (Fig. 2H). Regional climate data from Pumacocha indicate climate conditions drier than present from 6000 to 5000 cal yr BP that become progressively wetter after ~4500 cal yr BP (Fig. 2G). 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 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 (from ~0.003 to 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. 2E), a four-fold increase in total pollen accumulation (PAR), an 8% decline in trees and shrubs, a ~3% increase in palm pollen (*Mauritia*/*Mauritiella*, *Euterpe*, and *Oenocarpus*), an 18% increase in *Mauritia*/*Mauritiella* pollen accumulation, and the continued presence of maize pollen, (Fig. 2F, Fig. 3 SOM). Phytolith data from the archaeological soil profiles indicate the presence of manioc (*Manihot* sp.) and leren (*Calathea* sp.) crops (Fig. 2C). Burning is indicated by soil macrocharcoal (particles/cm^3) 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 ~2400 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. 2E), 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. 2F, 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. 2H), and the onset of slightly wetter, more variable precipitation conditions indicated by the δ^{18}O values from Pumacocha (Fig. 2G).

Early Versalles Phase (1100-800 cal yr BP)

After 1100 cal yr BP sedimentation decreases (from ~ 0.017 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. 2E, 2F, Fig. 3 SOM). Tree, shrub, and palm pollen are stable through this period (Fig. 2F). There is a 20% increase in herb phytoliths at the expense of trees and shrubs in the ADE/ABE soil profiles, however change in the local 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 (indicated by the 20% decrease in trees and shrub phytoliths), 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. 2H). Palaeoclimate exhibits drier conditions during this period associated with the MCA (1300-900 cal yr BP, Fig. 2G).

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. 2F). In the ADE/ABE soil profiles, there is an increase in biomass burning and forest clearance associated with increased soil macrocharcoal (particles/cm^3; 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 [75]. The development of these earthworks is associated with increased regional human activity indicated by increased SPD and site frequency values and earthwork construction (Fig. 2H). 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 [70,71] (Fig. 2H).

Discussion

Versalles in a Regional Palaeoecological Context

Through the early and mid-Holocene (~11,000 to 4000 cal yr BP), the presence of components of SDTF around LV is indicated by a key dry forest taxa *Anadenanthera* [94,95] (Fig. 3 SOM). High concentrations of *Isoetes* indicate lower lake levels [96] which is consistent with regional lake records that track drier conditions associated with the mid-Holocene Dry Event (MHDE) [97–101], including Laguna Bella Vista and Laguna Chaplin [10,102,103], Cuatro Vientos [104], Laguna Oricore [17,61], Lakes Chalalán and Santa Rosa [20], and Lake Rogaguado [105]. 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 [10,17,102–106]. These regional lakes were dominated by SDTF, savannahs, and gallery forest patches until the late Holocene (~4000 cal yr BP) 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 [10,17,102,103,106]. 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 did 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, were 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 from the onset of the record ca. 11,000 cal yr BP and begins to increase after 4500 cal yr BP. Drought conditions are a key factor in increased forest flammability in modern Amazon vegetation [107,108]. The natural occurrence of fire is low in rainforest systems as a result of the high fuel moisture [109]. 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 [60,110]. 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. 2G) [69].

Fire activity at LV increases slightly ~6000 cal yr BP a few hundred years prior to the first evidence of maize pollen (Fig. 2F, Fig. 3 SOM), a pattern common in other Amazon lakes [17,20,110–112]. 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. 2G). 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 altered palaeofire regimes [46]through the use of frequent, low severity fire for local forest clearance and 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 frequent burning as a tool to clear land for crop cultivation and increase soil fertility for nutrient-demanding crops such as maize [38,113,114].

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 [64,105,111,115–117]. 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 [105], and in the nearby Monte Castelo shell-mound ~5300 cal yr BP [4,118].

Polyculture Agroforestry and ADE/ABE Formation

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 [5,64] (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), is coupled with 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, which was 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 [60,61,64,110]. Previous analysis of the spatial distribution of anthropogenic soils at LV suggests ADE fertility was an unintentional bi-product of domestic waste [75], whereas ABE formed as the result of long-term soil enrichment through activities such as burning and mulching [38,42,44,119,120] and were focused on food production. The presence of maize and manioc intercropping [38,121–124] prior to the formation of ADE/ABE soils is consistent with the hypothesis of prolonged landscape domestication characterized by progressive soil enrichment [38] through the addition of waste, refuse, and charcoal [43,125]. 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 [75]. The presence of manioc in these small refuse middens or home gardens prior to the development of ABE soils at LV [75], support previous interpretations that manioc was domesticated in home gardens and only later expanded away from settlements with the development of larger ABE swiddens [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. 2H). 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 [104,126,127].

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) [4,118]. At MC, there is progressive land use diversification, rather than intensification through the Holocene [118]. However, at LV, the increase in land clearance, erosion, cultural burning, polyculture cultivation, and the later formation of ADE soils associated with domestic spheres and ABE soils associated with crop cultivation [75], 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 [26,27,29,31,128,129]. Coupled with significant climate variability associated with the MCA and LIA [70,130,131], intensive polyculture agroforestry (indicated by the continued enrichment in edible palm species and polyculture cultivation) and cultural burning (indicated by the presence of local and regional fire activity) persisted, suggesting stability in this land use system. 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 [5,132–134].

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) suggest 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. AD 1541 in Amazonia). This interpretation is supported by corroborating evidence of: (i) occupation following contact at Laguna Chaplin [10], Laguna San Jose [135] and Laguna El Cerrito [136], (ii) extensive archaeological evidence in the Bolivian lowlands [61,137,138], and (iii) European chronicles from the seventeenth century. In particular, Father Eder [139] and other chronicles [140] described sizeable populations living in large, well-planned fortified settlements and cultivating maize as one of the important crops.

Composition, Structure, and Cultural Burning in the ARE

Our data suggest ~5700 years of Indigenous cultural burning has persistent legacies of modern 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 [141]. 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 [53]. These modern ecological observations suggest that *M. flexuosa* stands have sufficient plasticity in reproductive output to sustain viable populations across a range of fire regimes [53]. The correlation with *M. flexuosa* PAR and charcoal influx values (Fig.2E-F) suggest that, the use of frequent, low severity 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 [142]. Ethnographic evidence from Amazonian Kayapo Indigenous groups of the Upper Xingu, 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 [59,142,143]. Previous research has proposed that the increase in palm-dominated stands of species such as *Attalea,* are an artifact of land use practices following the European encounter, including cattle ranching and large development projects [144]. Alternatively, other researchers have argued that *Attalea* is an indicator of human land use in pre-Columbian times [54,145]. 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 throughout 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 [93] that persisted through marked climate variability (i.e. the MHDE, MCA, LIA) and social change (Chocolatal, Early, and Late Versalles phases). 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 [75] demonstrate that modern ADE forests have lower canopy moisture and increased drought susceptibility [146], making them more fire prone. Recent research suggests that millennia of fire activity in forests in the southwestern 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]. While recent modelling studies suggest that 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 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 over five millennia. This resulted in altered vegetation composition and structure that is still detectable using modern remote sensing data. At present the anthropogenic forests of the Bolivian ARE remain protected as a national reserve and are stable under present disturbance and climate regimes. However, in the upcoming century, it is likely that the ARE will be increasingly susceptible to the compounding factors of climate change and land use intensification that are projected to increase fire activity in the ARE region.

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Data Accessibility

Supplementary data to this article can be found online at Zenodo open source repository at https://rs.figshare.com/collections/Supplementary_material_from_Legacies_of_Indigenous_land_use_and_cultural_burning_in_the_Bolivian_Amazon_rainforest_ecotone_/5861945.

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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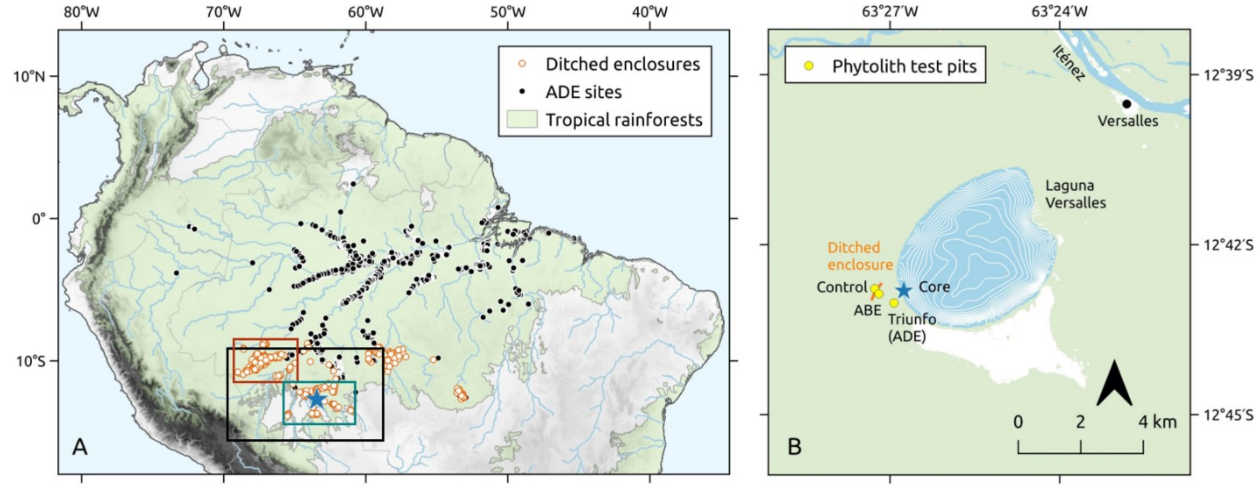

Figure 1. Regional Study Map Laguna Versalles. A: ARE region (black square), Southwestern Amazon (orange square), and Llanos de Moxos archaeological regions after [93], along with documented ADE sites (black dots) and ditched enclosures (orange circle) in Amazonia in the ARE. B: bathymetry of Laguna 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).

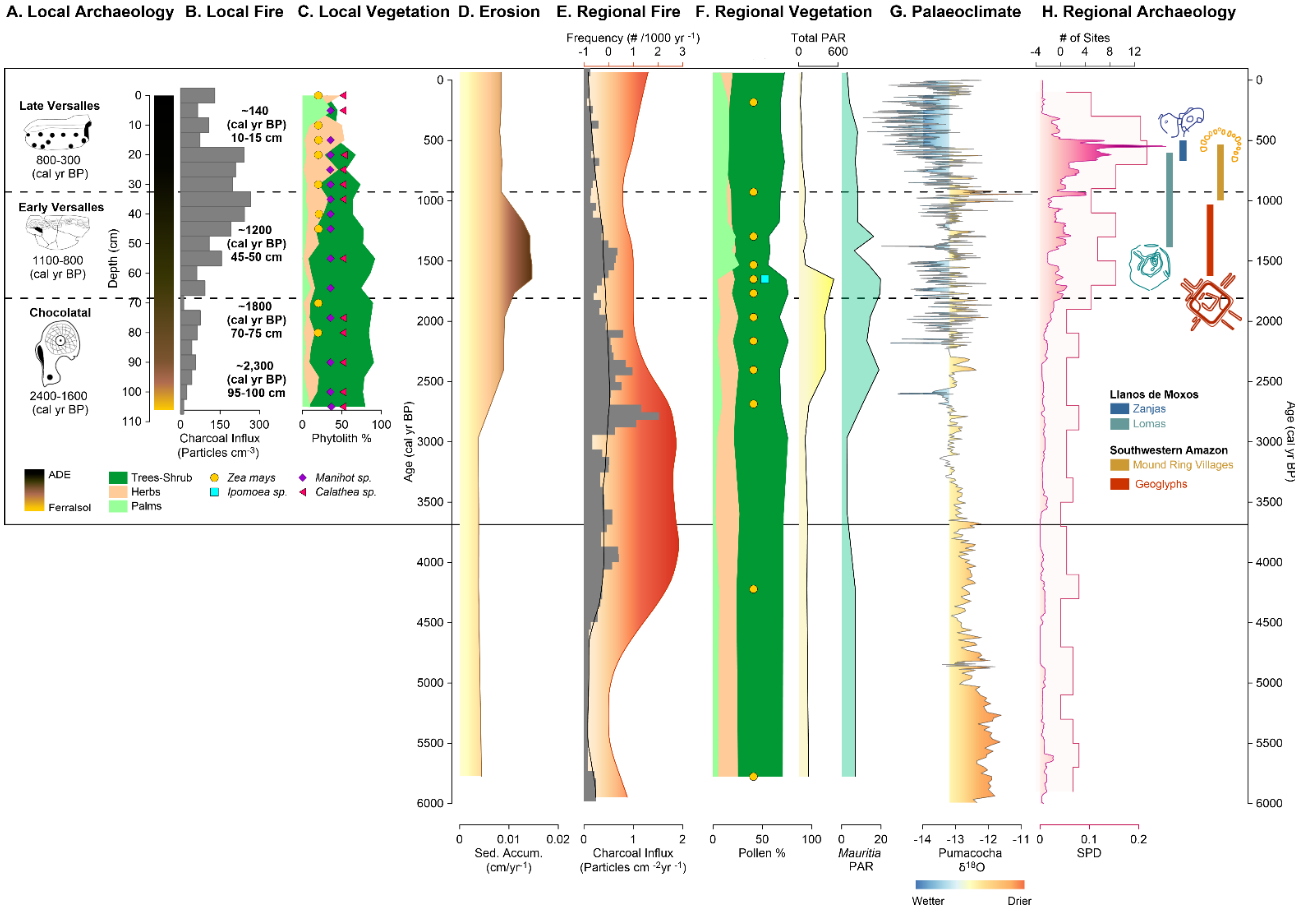

Figure 2. Laguna Versalles Data Summary. A. Local Archaeology summarizing the ceramic phases and ADE soil profile, B. Local Fire based on soil charcoal (grey), C. Local Vegetation and crops identified based on phytolith data, D. Erosion based on sediment accumulation from Laguna Versalles, E. Regional Fire based on lake sediment charcoal influx (grey) and CHAR Analysis [91] including background (black line) and fire frequency (orange fill), F. 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), G. Regional Palaeoclimate based on δ^{18}O from Pumacocha [69]. H. Regional Archaeology from the Bolivian lowlands based on previously published SPD values and number of archaeological sites (pink step-plot) modified from [10] plotted along with the occurrence of archaeological including Lomas (green) and Zanjas (blue) from the Llanos de Moxos region and Geoglyphs (orange) and Mound Ring Villages (yellow) from the southwestern Amazon region modified from [93]

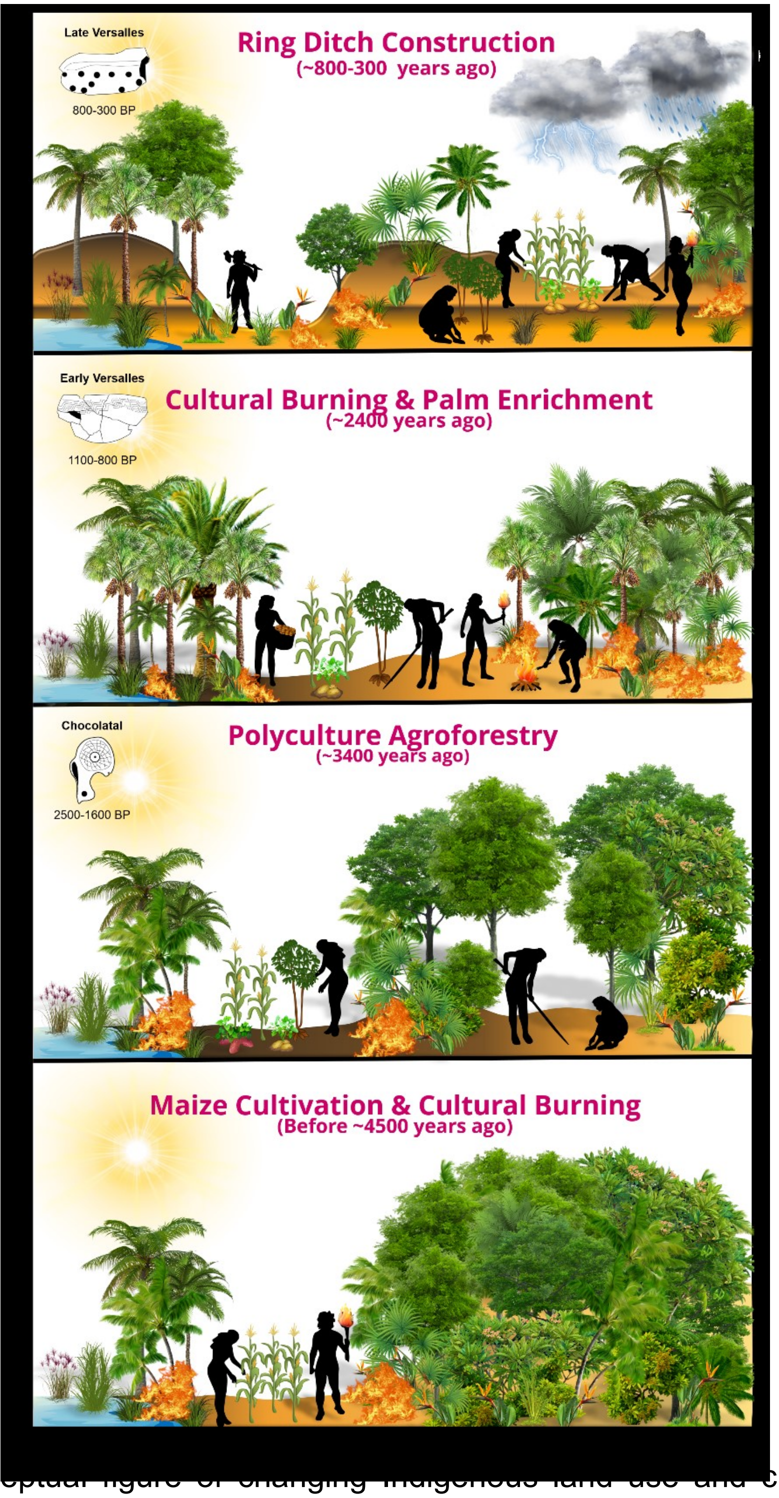

Figure 3. Conceptual figure of changing Indigenous land use and cultural burning at Laguna Versalles: including early maize cultivation and cultural burning, polyculture agroforestry, ADE/ABE soil formation and palm enrichment, and ring ditch construction.