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 harbour 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 ca 5700 cal yr BP. Polyculture cultivation of maize, manioc and leren after ca 3400 cal yr BP predates the formation of Amazonian Dark/Brown Earth (ADE/ABE) soils (approx. 2400 cal yr BP). ADE/ABE formation is associated with agroforestry indicated by increased edible palms, including *Mauritia flexuosa* and *Attalea* sp., and record levels of burning, suggesting that 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 in ADE/ABE forests in the ARE.

This article is part of the theme issue ‘Tropical forests in the deep human past’.

1. 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 harbours high-levels of habitat heterogeneity and biodiversity [1] and the SFS harbour 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 (greater than 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 coming decades, 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 that Indigenous land use and traditional burning practices (henceforth cultural burning [15]) influenced floristic composition and forest structure in the Amazon for millennia [6,16–22], particularly during the height of pre-Columbian Indigenous occupation [23–25] and earthwork construction (after approx. 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 (approx. 1300 km west of Laguna Versalles (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].

2. Material and methods

(a) Study site

We selected the Iténez Forest Reserve, a tract of ca 5000 km² 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 savannas. 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 savannas 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 [65–68].

Research was conducted in and around LV, a large (ca 21.6 km²) closed-basin, flat-bottomed lake, located ca 3 km southwest of the modern village of Versalles (12.66° S, 63.38° W, ca 146 m above sea level; figure 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 [76]. Archaeological and terrestrial palaeoecological research was conducted at the Triunfo site on the southwestern shore of LV, 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 llanos with a diameter at breast height (approx. 1.30 m above the ground) larger or equal to 10 cm were measured within 10 m of the transect line (electronic supplementary material, table S1). 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.

(b) Palaeoecology

In 2016, a 42 cm sediment core dating to ca 11 300 cal yr BP was collected from LV (12.42.45.6° S, 63.26.37.2° W; ca 600 m from the shore at a depth of 2.2 m) (figure 1a,b). The maximum lake depth was 2.8 m (figure 1b). Samples were taken from an anchored floating platform near the southwestern shore of the archaeological site of Triunfo, using a modified drop-hammer Colinvaux-Vohnout 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 (UK) and stored at 4°C.

(c) Age model
Age–depth relationships were modelled on five bulk sediment accelerator mass spectrometry (AMS) radiocarbon dates (electronic supplementary material, table S2) in a Bayesian framework using ‘BACON’ [79]. The latitudinal location of LV (12.7°S) is within the migration range of the inter tropical convergence zone (ITCZ) and has 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], thus the International Calibration Curve (IntCal20) Northern Hemisphere [80] versus Southern Hemisphere calibration curve [81] was selected for the radiocarbon calibrations. Radiocarbon ages were calibrated within Bacon v. 2.2 [83] in R [79,84,85].

The age–depth model mean accumulation rate priors were calculated within Bacon v. 2.2 [83] in R [79,84,85]. The age–depth model mean accumulation rate priors were calibrated within Bacon v. 2.2 [83] in R [79,84,85]. The age–depth model mean accumulation rate priors were calibrated within Bacon v. 2.2 [83] in R [79,84,85]. The age–depth model mean accumulation rate priors were calibrated within Bacon v. 2.2 [83] in R [79,84,85]. The age–depth model mean accumulation rate priors were calibrated within Bacon v. 2.2 [83] in R [79,84,85].

(d) 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 [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, UK 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 by using morphological and size criteria defined by Holst et al. [88]. Pollen types of cultigens and wild relatives of I. batatas are indistinguishable, but we are confident that the grains we report came from cultigens because: (1) wild species of these crops are 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.

(e) 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 analysed for charcoal pieces larger than 125 μm using a modified macroscopic sieving method [89]. 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 greater than 125 μm in diameter) was counted in a gridded Petri dish at 40× 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). CHARAnalysis statistical software (http://phiguera.github.io/CharAnalysis/) 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.

(f) Archaeology
A four-week archaeological excavation was conducted in 2017 at the archaeological site of Triunfo located on the southwest shore of LV (figure 1) to recover cultural material, establish construction chronology of earthworks and assess site formation history [76]. Ceramic material was analysed following standard procedures to assess changes in form, paste and decoration, and compared to regional collections (electronic supplementary material, figure S1). Ceramic analysis consisted of observing the fresh fractures of 1044 ceramic fragments under binocular loupes (10 to 25× magnification). The classification of ceramic
3. Results

To contextualize the history of human–environment interactions at Versalles, the palaeoecological and archaeobotanical reconstructions for the past ca 6000 years are interpreted alongside new ceramic and earthwork constructions for the past ca 4000 cal yr BP. 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 (approx. 1100–800 cal yr BP) and Late Versalles (800–300 cal yr BP); electronic supplementary material, figure S1). The phases are recognizable by morphological and decorative attributes, not including paste, which generally contains ground ceramic (chamote), ground quartz, cauxi (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 (electronic supplementary material, table S3); however, as the site was only partially excavated, it is possible that these chronological boundaries may change after future excavations.

(b) 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 (less than 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 over 40% Moraceae/Urticaceae pollen in the record. The presence of less than 1% of Anadenanthera (electronic supplementary material, figure S3), 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 are unlikely to have derived from long-distance transport. Maize pollen is present after ca 5700 cal yr BP (figure 2f) along with onset of low levels of fire activity (figure 2e), and is consistent with low levels of regional human activity indicated by the SPD and site frequency data (figure 2h). Regional climate data from Pumacocha indicate climate conditions drier than the present (from 6000 to 5000 cal yr BP) that become progressively wetter after ca 4500 cal yr BP (figure 2g). Drier conditions likely promoted lower lake levels, which in turn supported high concentrations of the emergent macrophyte Isoetes (greater than 60%, (electronic supplementary material, figure S3)). Regional climate gets progressively wetter after ca 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 ca 4500 cal yr BP, reaching record levels ca 2800 cal yr BP.

(c) The Chocolatal ceramic phase and ADE formation (before 2400–1600 cal yr BP)

Sediment accumulation begins to increase (from ca 0.003 to 0.007 mm yr\(^{-1}\)) between 3000 and 2400 cal yr BP (figure 2d) coupled with an increase in fire activity ca 2800 cal yr BP (figure 2e), a four-fold increase in total pollen accumulation (PAR), an 8% decline in trees and shrubs, a ca 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 (figure 2f, electronic supplementary material, figure S3). Phytolith data from the palaeoecological soil profiles indicate the presence of manioc (Manihot sp.) and leren (Calathea sp.) (figure 2e). Burning is indicated by soil macrocharcoal (particles/cm\(^2\)) found after approximately 2400 cal yr BP, prior to the formation of anthropic soils and present throughout the soil profiles once the ADE/ABE soils form (figure 2b); electronic supplementary material, figures S5–S8). ADE/ABE soil formation begins ca 2400 cal yr BP during the Chocolatal ceramic phase (figure 2a; electronic supplementary material, figure S1, §1. Triunfo Ceramics). The highest recorded sediment accumulation at LV occurs between ca 1700 and 1100 cal yr BP (approx. 0.017 mm yr\(^{-1}\); figure 2d) coupled with an increase in biomass burning (figure 2e), decrease in both total PAR and Mauritia/Mauritiella PAR values, a ca 20% decline in trees and shrubs, the continued presence of maize and sweet potato (Ipomoea sp.) pollen and more than 10% increase in palms (Mauritia/Mauritiella, Attalea, Euterpe and Oenocarpus, figure 2f; electronic supplementary material, figure S3). This period corresponds with increased regional human activity indicated by the increase in SPD and site frequency values after ca 2400 cal yr BP (figure 2h), and the onset of slightly wetter, more variable precipitation conditions indicated by the \(\delta^{18}O\) values from Pumacocha (figure 2g).
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 CHARAnalysis [91] including background (black line) and fire frequency (orange fill). (f) Regional vegetation based on pollen data grouped into trees–shrubs (dark green), herbs (beige), palms (light green) and crop pollen identified, total pollen accumulation rate (PAR; yellow) and Mauritia PAR (light teal), (g). Regional palaeoclimate based on $\delta^{18}O$ 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 Zanjias (blue) from the Llanos de Moxos region and geoglyphs (orange) and mound ring villages (yellow) from the southwestern Amazon region modified from [73]. (Online version in colour.)

(d) Early Versalles phase (1100–800 cal yr BP)

After 1100 cal yr BP, sedimentation decreases (from approx. 0.017 to 0.008 mm yr$^{-1}$) (figure 2d), synchronous with a decline in burning and maize pollen was only recorded in one sample from LV ca 920 cal yr BP (figure 2e,f; electronic supplementary material, figure S3). Tree, shrub and palm pollen are stable through this period (figure 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 (figure 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 (figure 2c). The increase in forest clearance (indicated by the 20% decrease in trees and shrub phytoliths) associated with the Early Versalles ceramic phase (ca 1100 to 800 cal yr BP; figure 2a, (electronic supplementary material, figure S1. §1.Triunfo Ceramics) corresponds to an increase in regional human activity indicated by the SPD and site frequency values (figure 2h). Palaeoclimate exhibits drier conditions during this period associated with the MCA (1300–900 cal yr BP; figure 2g).

(e) The Late Versalles and ring ditch phase

(800–300 BP)

After 800 cal yr BP, sediment accumulation remains stable (approx. 0.008 mm yr$^{-1}$; figure 2d) in the upper portion of the lake record accompanied by low levels of biomass burning with maize pollen only present in one modern sample (ca 180 cal yr BP; figure 2f). In the ADE/ABE soil profiles, there is an increase in biomass burning and forest clearance associated with increased soil macrocharcoal (particles cm$^{-2}$); figure 2c, electronic supplementary material, figures S5–S8), declines in arboreal phytoliths and increase in the proportion of herb phytoliths. Maize, manioc and leren phytoliths indicate continued crop cultivation at the site (figure 2; electronic supplementary material, figures S5–S8). This intensification of ADE land use is associated with the Late Versalles ceramic phase (ca 800 to 300 cal yr BP; figure 2a, electronic supplementary material, figure S1. §1.Triunfo Ceramics) and 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 indicated by increased SPD and site frequency values and earthwork construction (figure 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] (figure 2f).

4. Discussion

(a) Versalles in a regional palaeoecological context
Through the early and Mid-Holocene (approx. 11,000 to 4000 cal yr BP), the presence of components of SDTF around LV is indicated by a key dry forest taxa Anadenanthera [93,94] (electronic supplementary material, figure S3). High concentrations of Isoetes indicate lower lake levels [95], which is consistent with regional lake records that track drier conditions associated with the Mid-Holocene dry event (MHDE) [96–100], including Laguna Bella Vista and Laguna Chaplin [10,101,102], Cuatro Vientos [103], Laguna Oricore [17,61], Lakes Chalalán and Santa Rosa [20] and Lake Rogaguado [104]. However, despite the presence of this key SDTF taxa at LV, the presence of over 40% Moraceae/Urريمexaceae and under 20% Poaceae pollen throughout the Holocene indicates a greater abundance of TFRF vegetation compared with existing regional lake records [10,17,101–105]. These regional lakes were dominated by SDTF; savannahs and gallery forest patches until the late Holocene (approx. 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 past 50,000 years [10,17,101,102,105]. Despite being along the ARE boundary, the continued dominance of TFRF at LV suggests a stable rainforest ecosystem throughout the Holocene (electronic supplementary material, figures S3–S4). 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, where early occupants could exploit a range of vegetation types and resources.

(b) 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 Amazonian vegetation [106,107]. The natural occurrence of fire is low in forest ecosystems as a result of the high fuel moisture [108]. As a result of the low incidence of natural fire, the occurrence of fire in rainforest ecosystems has previously been interpreted as human-caused fire activity [60,109]. If drought was the dominant driver of fire at LV, the highest fire activity would be associated with the driest climate conditions ca 6000–5000 cal yr BP (figure 2g) [69].

Fire activity at LV increases slightly ca 6000 cal yr BP, a few hundred years prior to the first evidence of maize pollen (figure 2f; electronic supplementary material, figure S3), a pattern common in other Amazon lakes [17,20,109–111]. 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 toward wetter regional climate conditions (figure 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 [81]. Thus, the synchronous onset of fire activity combined with the presence of maize pollen suggests that 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 use the nutrient-rich soils around the lake shore for maize cultivation (figure 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 [38,112,113].
The occurrence of maize pollen at LV after ca 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 [64,104,110,114–116]. Earliest maize in the region appears ca 6850 cal yr BP in anthropic forest islands of the seasonally flooded savannahs to the southwest of Triunfo [3], Lake Rogaguado ca 6500 cal yr BP [104] and in the nearby Monte Castelo shell-mound ca 5300 cal yr BP [4,117].

(c) Polyculture agroforestry and ADE/ABE formation

Land use intensification begins after ca 2800 cal yr BP associated with a progressive increase in erosion (indicated by increased sediment accumulation rates) and 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 ca 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 associated with cultural burning likely represents the antecedent conditions for the establishment of polyculture agroforestry, which was later followed by ADE/ABE soil formation at LV (ca 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 [60,61,64,109]. Previous analysis of the spatial distribution of anthropogenic soils at LV suggests that ADE fertility was an unintentional byproduct of domestic waste [76], whereas ABE formed as the result of long-term soil enrichment through activities such as burning and mulching [38,42,44,118,119] that were focused on food production. The presence of maize and manioc intercropping [38,120–123] 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 refuse and charcoal [43,124]. Similar to the hypothesis proposed by Arroyo-Kalin [38], 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 around LV (ca 2400 cal yr BP) [76,125]. The presence of manioc in these small refuse middens or home gardens prior to the development of ABE soils at LV [76] supports 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 (figure 2b–f and figure 3). This land use intensification occurs during the transition between the Chocolatal and Early Versalles ceramic phases (ca 1600 to 1300 cal yr BP; figure 2a, electronic supplementary material, figure S1. §1.Triunfo Ceramics) and corresponds to a decrease in regional human activity indicated by lower SPD and site frequency values (figure 2b). The cultural transformation associated with the decrease in regional human activity and the distinct transition from Chocolatal to Early Versalles cultural phases are 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 [103,126,127].

The exploitation of a diverse range of cultivated, managed and wild species is similar to subsistence strategies documented for the past 6000 years at the nearby site of Monte Castello (MC, ca 40 km away) [4,117]. At MC, there is progressive land use diversification, rather than intensification through the Holocene [117]. 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 [76] suggest that land use practices were both diversifying and intensifying during the Late Holocene. This may be attributed to the increased availability of terre firme land at LV compared with the raised mound of MC, which is one of the only areas of terra firme available for kilometres during the wet season [117].

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 (figure 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. ARE land use is 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] suggesting stability in this land use system.

Furthermore, the continued presence of maize pollen until ca 180 cal yr BP and maize and manioc phytoliths after ca 140 cal yr BP (figure 2c) 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 AD 1541 in Amazonia). This interpretation is supported by corroborating evidence of (1) occupation following contact at Laguna Chaplin [10], Laguna San Jose [135] and Laguna El Cerrito [136], (2) extensive archaeological evidence in the Bolivian lowlands [61,137,138] and (3) 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.

(d) Floristic composition, forest structure and cultural burning in the ARE

Our data suggest that ca 5700 years of Indigenous cultural burning left persistent legacies in modern floristic composition and forest 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 (figure 2c,f) suggests 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 cryptogal 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 [39,142,143]. Previous research proposed that the increase in palm-dominated stands of species such as *Attalea* is an artefact 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 ca 2000 cal yr BP at LV suggests that palm-dominated stands originated during the cultural transition between the Chocolatal and Early Versalles phases associated with Indigenous cultural burning and polyculture agroforestry, ca 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) scales. 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.

(e) The legacy of humans in the ARE and modern management implications

The data from LV suggest that polyculture agroforestry and cultural burning formed a stable land use system [75] 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 more than 40% of rainforest pollen throughout the record, despite the continued enrichment in palms after ca 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 [146], making them more fire-prone. Recent research suggests that millennia of fire activity in forests in the southwestern Amazon may have preconditioned these forests to be more resilient to the threat of increased modern fire activity, as 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 of 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 coming decades [13].

5. Summary

The data from LV indicate both a stable rainforest ecosystem and stable land use system 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 floristic composition and vegetation structure that are still detectable using modern remote sensing data. At present, these anthropogenic forests of the Bolivian ARE remain protected as a national reserve and are stable under present disturbance and climate regimes. However, in the coming decades, 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.

Data accessibility. Supplementary data to this article can be found online in the publicly available Neotoma database (www.neotomadb.org) and Global Charcoal database (www.gpwg.org/gpwpdb.html) once these data are published.

Authors’ contributions. S.Y.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; S.E.: data curation, formal analysis, investigation, writing—review and editing; M.R.: conceptualization, data curation, formal analysis, investigation, methodology, writing—review and editing; C.J.B.: data curation, formal analysis, investigation, writing—review and editing; J.G.S.: formal analysis, investigation, methodology, visualization, writing—review and editing; D.A.: data curation, formal analysis, investigation, writing—review and editing; M.G.: formal analysis, investigation, writing—review and editing; L.H.: formal analysis, investigation, writing—review and editing; D.H.U.: conceptualization, data curation, formal analysis, investigation, methodology, resources, supervision, writing—review and editing; W.D.G.: resources, supervision, writing—review and editing; J.I.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing.

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Competing interests. We declare we have no competing interests.

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