Journal of Archaeological Science 130 (2021) 105382

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: http://www.elsevier.com/locate/jas

Insights into past land-use and vegetation change in the Llanos de Moxos (Bolivia) using fungal non-pollen palynomorphs

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ARTICLE INFO

Keywords:
Pre-Columbian
Palaeoecology
Amazon
Llanos de Moxos
Raised-field agriculture
Non-pollen palynomorphs
Fungi

ABSTRACT

Here we document a 1000-year fungal record from the raised-field region of the Llanos de Moxos, a seasonally inundated forest-savanna mosaic in the Bolivian Amazon. Fungi are extremely sensitive to changes in vegetation due to their close relationship with the local environment, providing a useful proxy for past local vegetation and land-use change. Here the remains of fungal non-pollen palynomorphs (NPPs) are identified from a sediment core taken from Laguna El Cerrito. A multivariate constrained ordination is used to extract relationships between the fungal NPP types and environmental gradients, specifically, tree cover, near-shore vegetation, crop cultivation, burning and local sediment input. NPP types such as *Neurospora* cf. *cerealis* are identified as indicative of pre-European agriculture and offer the ability to expand on the temporal range of cultivation in the raised-field region. Constrained cluster analysis indicates that the most significant changes in the NPP assemblage occurs c. 1500 and c. 1700 CE, corresponding to the arrival of Europeans to the Americas and Jesuit missionaries to the Llanos de Moxos respectively. The modern savanna landscape is one shaped by changes in land-use and the introduction of cattle following the European Encounter.

1. Introduction

Indigenous peoples have inhabited the Llanos de Moxos (or simply 'Moxos') region of Bolivia for at least the last 10,000 years, cultivating crops and using fire to manage the landscape (Brugger et al., 2016; Capriles et al., 2019; Lombardo et al., 2020). Across this vast seasonally-inundated tropical savanna distinct cultural groups built earthworks in the form of raised fields, mounds, ring ditches, canals, causeways, fish weirs, and artificial forest islands, dating back at least 2500 years (Denevan, 1966; Erickson, 2000, 2006; Jaimes Betancourt, 2012; Lombardo et al., 2011; Prestes-Carneiro et al., 2019; Walker, 2004, 2008, 2018). In the last c. 500 years indigenous depopulation, changes in demography, the introduction of cattle ranching, intensive agro-industrial farming and anthropogenic climate change has led to changes in its ecosystem structure and function. However, the extent to which the vegetation of the *Moxos* has been modified by people, at least at a regional scale, and when or if it was transformed into an intensively cultivated anthropogenic landscape is still debated (Erickson, 2008; Heckenberger et al., 2003; Langstroth, 2011; Mayle et al., 2007).

Palaeoecological and environmental archaeological investigations using pollen preserved in sediments have been used across *Moxos* to help refine our understanding of past vegetation change, plant domestication an indigenous land-use practices (Brugger et al., 2016; Carson et al., 2014; Whitney et al, 2013, 2014). However, the investigation of non-pollen palynomorphs (NPPs) - the material that is not pollen in palynological samples - has yet to be incorporated into these reconstructions, which can provide an important new and supporting data source. NPPs have been successfully used to examine changes in pastoral and grazing activity (Cugny et al., 2010; Gauthier et al., 2010; Gill et al., 2013; van Asperen et al., 2020), herbivore extinctions (Davis, 1987; Gill et al., 2009), fire frequency (Stivrins et al., 2019), Neolithic woodland management (Innes et al., 2010), human landscape modification

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https://doi.org/10.1016/j.jas.2021.105382
Received 29 January 2021; Received in revised form 22 March 2021; Accepted 8 April 2021
Available online 23 April 2021
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(Willemsen et al., 1996) and aid in reconstructing Norse (Schofield and Edwards, 2011) and Roman settlements (van Geel et al., 2003). While their use was initially developed in northern temperate peat bogs (van Geel, 1972, 1976, 1978) their incorporation into the reconstruction of past ecosystems in tropical South America has increased substantially in the last decade (Leal et al., 2019; Loughlin et al., 2018; Medeanic and Silva, 2010; Montoya et al, 2010, 2011, 2012; Musotto et al., 2017; Nuñez Otaño et al., 2017; Stutz et al., 2010). NPPs typically consist of fungal remains (specifically those of Ascomycetes, Basidiomycetes and Zygomycetes), cyanobacteria, algae, testate amoebae, dinoflagellate cysts, nematodes, rotifers, and tardigrades (Heitman et al., 2017; Medeanic and Silva, 2010; Shumilovskikh and van Geel, 2020). Fungal remains are a particularly useful proxy for disentangling past local vegetation change due to the close relationship between fungi and their specific host or substrate (Peay et al., 2013) and the short distance the fungal remains travel (van Geel and Aptroot, 2006). The application of fungal remains, to palaeoecological and archaeological questions has continued to expand as their utility in interpreting the past is realised (der Linden et al., 2012; Haas, 2010; van Geel, 2001).

Here we present the first fungal non-pollen palynomorph record from Bolivia and use it to investigate 1000 years of land-use change in the raised field region of the *Moxos*. This study aims to (1) identify the key fungal taxa from the seasonally-inundated savanna of northern Bolivia, (2) incorporate these fungal NPPs into a multiproxy reconstruction of land-use change in the Moxos, and (3) identify specific fungal taxa that can be used to aid in reconstructing periods of pre-Columbian raised field agriculture.

2. Study site

2.1. Llanos de Moxos

The *Moxos* region is a centre of biodiversity and crop domestication within the world's largest protected wetlands complex at 6.9 million hectares (RAMSAR, 2020). Located centrally within South America, with the Andes mountains to the west and the Precambrian shield to the east the region constitutes a vast (130,000 km^2) seasonally inundated savanna, interspersed with forest islands, and crossed by riparian-forested rivers (Fig. 1). The savanna has very little topographical relief, with a gradient of 10–15 cm km^{-1}, meaning that small differences in elevation can have marked effects on the hydrology and subsequently vegetation of large areas (Lombardo et al., 2013). High annual precipitation (1500–2000 mm per annum) during the rainy season (October to April) peaks in December–February when precipitation can reach >300 mm in a month, resulting in major flooding through March and April (Hanagarth, 1993; Hijmans et al., 2005). The seasonality of rainfall and flooding causes major changes in the landscape, as many lakes are connected to navigable rivers for several months, seasonal *arroyos* fill and dry out, and water stands for months with an area of 80,000–90,000 km^2 subject to inundation (Hamilton et al, 2002, 2004). The clay rich soils of the savanna source their parent material from weathering of the underlying sediments and in part from the Andes. Flooding is primarily caused by local precipitation rather than rivers overflowing, and as such the poorly drained, highly weathered, lateritic soils receive little new alluvial material (Boixadera et al., 2003; Lombardo et al., 2013). *Moxos* is a centre of grass (Poaceae) richness, particularly in species from the Panicoideae subfamily, which dominate the drier areas, while sedges (Cyperaceae) are more abundant in the wetter areas (Haase and Beck, 1989; Meneses et al., 2014). A few small trees and woody shrubs can be found scattered across the savanna, e.g. *Curatella americana* (Dilleniaceae) and *Vernonia* (Asteraceae). While more forested regions are divided between riparian forests, which flood every year, and dry forests, many of which are found on distinctive forest islands. Today, economic activity centres around cattle ranching and mechanised agriculture, with a primarily human-induced fire regime that opens the savanna for grazing.

2.2. Laguna El Cerrito

Laguna El Cerrito (here on referred to as LEC) is situated

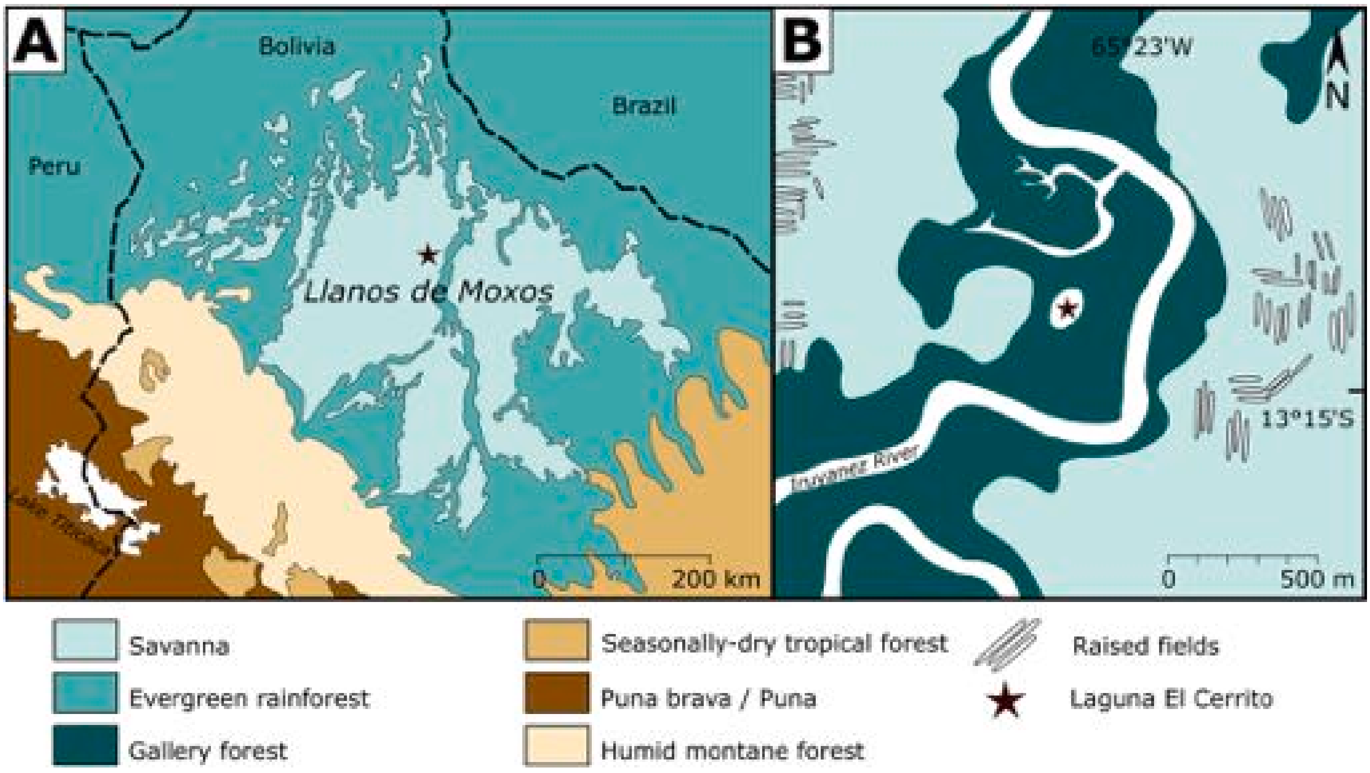

Fig. 1. Map of Northern Bolivia (A) showing the Llanos de Moxos and (B) location of Laguna el Cerrito (LEC).

approximately 55 km north of the town of Santa Ana de Yacuma, capital of the Yacuma Province (Fig. 1). LEC is a shallow (c. 1.10 m), 1000 m^2, oxbow lake situated on a meander of the Iruyañez River, at 138 m asl. The surrounding vegetation consists primarily of seasonally inundated riparian forest and is characterised by the trees *Vochysia mapirensis* (Vochysiaceae), *Duguetia quitarensis* (Annonaceae) and *Faramea occidentalis* (Rubiaceae), and the bamboo *Rhipidocladum* (Poaceae). A rapid vegetation survey of the micro habitat around LEC can be found in Whitney et al. (2014). The wider archaeological landscape includes expanses of raised fields and forest islands, stretching over more than 10,000 km^2, and including at least 45,000 fields and c. 2000 forest islands, of which three in every four forest islands show some evidence of pre-Columbian habitation (Walker, 2018). The most prominent archaeological site near to LEC (c. 2 km north-west) is the El Cerro rock formation. This large forest island (ca. 10 ha) reaches 40 m high and is surrounded by 100 ha of forest. Archaeological excavations indicate at least 8–20 ha of this forest contain evidence of pre-Columbian human activity based on a suite of seven radiocarbon dates which help define the “Cerro” Phase for the region, c. 1200–1500 CE (Walker, 2004, 2008, 2018). Test excavations at El Cerro recovered a stone axehead, dense concentrations of ceramics (200 sherds per m^3 of soil) and a dark soil colour with burned clay, all of which are diagnostic of pre-Columbian habitation (Walker, 2004). Archaeological evidence supports contemporary Jesuit written accounts of an indigenous leader associated with several settlements of between 1800 and 2000 inhabitants in the region (Walker, 2018). The agricultural history of this landscape is complex and includes relationships with at least six other distinctive constructed landscapes in *Moxos* alone. Regardless of the interpretation of the El Cerro forest island, the West Central Moxos landscape was densely inhabited, especially between 1300 and 1500 CE (Walker, 2018).

3. Methods

3.1. Core collection

In 2010, an 85 cm sediment core was recovered from LEC (13°14′50″ S, 65°23′09″ W). The sediment core was taken in the centre of the lake from a floating platform using a Colinvaux-Vohnout modified Livingstone piston corer (Colinvaux et al., 1999; Livingstone, 1955), together with a Perspex tube and piston to collect the uppermost soft sediments. Once recovered, the overlapping cores were sealed and returned to Edinburgh University (UK) intact for cold storage and subsampling. The LEC sediments were selected for investigation as they already contain a pollen and charcoal record (Whitney et al., 2014), allowing the fungal NPP assemblages to be interpreted alongside evidence of past changes in land use and vegetation.

3.2. Chronology

Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating was undertaken at the base of the core, then later after pollen analysis had been completed, *see* (Whitney et al., 2014) at the two most prominent changes in pollen composition (Table 1). The Bayesian statistical package ‘Bacon’ (Blaauw and Christen, 2011) was used within the ‘R’ statistical computing environment (R Core Team, 2020) to construct an age-depth model. Northern (IntCal20) (Reimer et al., 2020) and southern hemisphere (SHCal20) (Hogg et al., 2020) atmospheric curves were combined to create a mixed curve (50:50 mix) for radiocarbon calibration. This type of mixed curve is more representative of the tropics, where air masses mix from both the northern and southern hemisphere through the year following the movement of the Inter-Tropical Convergence Zone (Marsh et al., 2018). The model was also pinned to the year of coring (2010 CE) at 0 cm. Default priors were used in Bacon to produce 17 vertical sections of 5 cm thickness. The accumulation rate (acc.mean) was changed to 10 yr/cm as recommended by Bacon.

3.3. Fungal non-pollen palynomorphs

A total of 17 samples were examined for fungal NPP remains at regular 5 cm intervals, starting at the surface, through the LEC core. Samples were processed using a standard palynological protocol, including the use of hydrofluoric acid (HF), potassium hydroxide (KOH), hydrochloric acid (HCl) and acetolysis (Fægri and Iversen, 1989). An additional sieving step was included to concentrate crop pollen (Whitney et al., 2012). Exotic markers were added to the samples (*Lycopodium* (Batch 938934 = 10,679 ± 426 per tablet)) to estimate fungal NPP concentrations (Stockmarr, 1971). Residues were then mounted on glass slides in silicon oil and counted on a Nikon Eclipse 50i microscope at 400x and 1000x magnification. Fungal NPPs were counted until 100 exotic *Lycopodium* spores were found in each sample (fungal NPPs = 148–703; mean 306; total 5216). Identification of fungal remains was undertaken using the available literature (Cugny et al., 2010; Ellis, 1971, 1976; Ellis and Ellis, 1997, 1998; Gelorini et al., 2011; Guarro et al., 2012; Seifert et al., 2011; van Geel and Aptroot, 2006) and comparisons with material held in collections at Morehead State University.

3.4. Palaeoenvironmental proxies

To understand the changes in the fungal NPP proxy data through time five local environmental variables were identified as the likely contributors of assemblage change. These included 1) tree cover, 2) near-shore vegetation, 3) crop cultivation, 4) burning and 5) local sediment input. To explore these variables, five representative proxy records were sampled consisting of 1) tree pollen (Moraceae/Urticaceae, Combretaceae/Melastomataceae, Myrtaceae, *Cecropia*, *Ouratea*, *Celtis*), 2) sedge pollen, 3) *Zea mays* pollen, 4) macrocharcoal fragments (>250 μm) and 5) sediment organic content (loss-on-ignition). Pollen and charcoal data were extracted from Whitney et al. (2014). A conservative approach to crop cultivation was chosen using only *Zea mays* pollen despite *Ipomoea batatas* and *Inga* sp. pollen being identified. This selection was made as *Zea mays* pollen has defined morphological characteristics while both *Ipomoea* sp. and *Inga* sp. have morphologically similar species which are not cultivars. To establish the local organic input, sediment samples underwent a standard loss-on-ignition (LOI) protocol (Heiri et al., 2001). Samples of c. 2 cm^3 were dried at 80 °C for up to 12 h to remove moisture then weighed. This was then followed by a controlled burn at 550 °C for 4 h to remove organic carbon. Weight loss was then converted to a percentage of the dry weight to determine the proportion of organic carbon within the sediment.

Table 1
Radiocarbon ages obtained from LEC. Dates calibrated in Bacon (Blaauw and Christen, 2011) using a mixed IntCal20 (Reimer et al., 2020)/SHCal20 (Hogg et al., 2020) atmospheric curve.

Publication Code	Sample Depth (cm)	Material	$\delta^{13}C_{VPDB}$ (‰)	Uncal. radiocarbon age (yr B.P. ± 1σ)	Cal. radiocarbon age (yr (C.E.) ± 2σ)	Calendar age (C.E.) (weighted mean)
SUERC-35219	40	Sediment	−23.0	471 ± 37	1606–1406	1470
Beta-345409	55	Sediment	−18.7	670 ± 30	1390–1278	1333
SUERC-43152	80	Twig	−28.4	1010 ± 38	1176–984	1081

3.5. Zonation

All data processing and analysis was undertaken in the ‘R’ statistical computing environment (R Core Team, 2020). A stratigraphically constrained cluster analysis (CONISS) was performed on pollen percentage data and square-root transformed fungal NPP percentage data, first by calculating a dissimilarity indices using the Bray-Curtis method and then constrained hierarchical clustering (CONISS). The dendrograms were produced using the ‘chclust’ function in the package ‘vegan’ (Oksanen et al., 2019). These were then tested against a broken stick model to obtain the number of zones (Bennett, 1996). The pollen and fungal NPP data, and their respective zones were then plotted using the ‘strat.plot’ function in the package ‘rioja’ (Juggins, 2017).

3.6. Constrained ordination

Canonical Correspondence Analysis (CCA) (ter Braak, 1986) was used to investigate the relationship between fungal NPPs and the five selected environmental variables. The fungal NPP percentage data and environmental variable data were first square-root transformed to compensate for the variable scales of environment data and compensate for abundant taxa, which occur in proxies with low dispersal potential, such as fungal NPPs (Wilmshurst and McGlone, 2005). The package ‘vegan’ (Oksanen et al., 2019) was used to extract the explanatory power (inertia/variance) of the environmental variables and the eigenvalues (λ_i) of each constrained axis. The CCA was then plotted using scaling focused on the species (species scores scaled by λ_i). Linear dependencies between the environmental variables were investigated using Variance Inflation Factors (VIF) to determine any indication of collinearity. VIF is a measure of how much the variance of the regression coefficients is exaggerated by the presence of the other environmental variables. Initially a grass pollen variable was included in the analysis, however, this led to a high collinearity between the grass and forest pollen environmental variables (VIF > 20) suggesting that they are almost entirely explainable by each other. This was observable as a strongly inverse relationship between grass and tree pollen in a test CCA. Removal of the redundant environmental gradient (grass pollen) produced a VIF < 5 for all remaining environmental gradients indicating little collinearity remained.

3.7. Permutation tests

Permutation tests were undertaken using the package ‘vegan’ (Oksanen et al., 2019) to determine how much of the variation is explained by the model in comparison to that of a null distribution using the function *permustats*. To test the overall significance of the model an *F* statistic was generated for the observed model and compared to that of 999 permuted models, where species data were reshuffled. The *anova* function was then used to test the significance of the variation in fungal NPPs as explained by the environmental variables. In addition to the base CCA with five prechosen environmental variables a stepwise selection method was used to attempt model selection (Blanchet et al., 2008). The *ordeiR2step* function was then used which first tests all environmental variables, then proceeds with a stepwise selection using a significance threshold ($\alpha \leq 0.05$) and an R^2 adjusted for the number of variables. This reduced model was then examined to see if the smaller subset of environmental variables still explained the data.

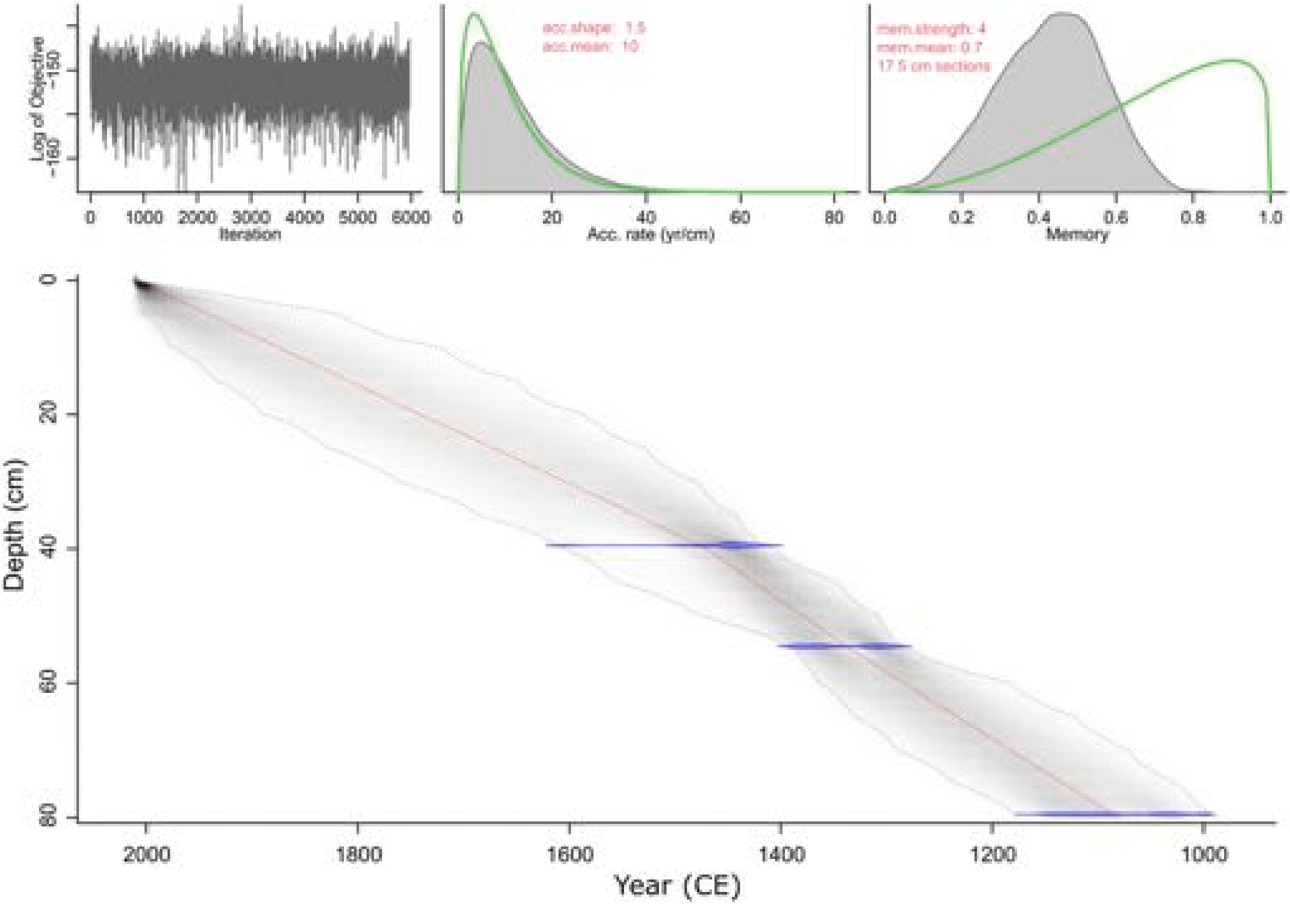

Fig. 2. Age-depth model for LEC. Model created in the ‘R’ statistical computing environment (R Core Team, 2020) using the package Bacon (Blaauw and Christen, 2011).

4. Results

4.1. Chronology

The chronology established is based on three AMS ^{14}C dates and pinned to 0 cm at the year of coring (Table 1). The mean ages generated by Bacon at every centimetre of the core are used to construct the age-depth model (Fig. 2).

4.2. El Cerrito palaeoecology

Pollen and charcoal data from Whitney et al. (2014) is replotted with sediment organic content data and zones established using CONISS and the new age-depth model. Zonation identified three distinct pollen assemblage boundaries located between samples 62–65 cm (midpoint date c. 1250 CE), 52–55 cm (midpoint date c. 1350 CE) and 35–37 cm (midpoint date c. 1520 CE) (Fig. 3).

Seventy-eight distinct morphological fungal NPP types were identified from the LEC core, of which fifty-two met the requirements of the presence (≥2% abundance in one sample) and persistence (in ≥2 samples) filters (Plate 1). All morphological types were assigned to previously described forms or given descriptive names. Zonation identified two boundaries located between samples 35–40 cm (midpoint date c. 1500 CE) and 20–25 cm (midpoint date c. 1700 CE) (Fig. 4).

4.2.1. Zone NPP-1 (1080–1500 CE)

Fungal NPPs within the earliest part of the record are dominated by the forms cf. *Coprinus* sensu lato (18–33%) and *Arthrinium*-type (19–41%) forms, with supplementary *Drechslera-Bipolaris*-type (1–12%), Bulbil shaped (1–9%), cf. *Xylomyces aquaticus* (0–7%), Indet. fungal spore 1 (4–8%) and *Anthostomella*-type (0–6%). Fungal NPP concentration range from 24,135–75,073 (mean = 44,104) spores per cm^3. Pollen consists predominantly of grasses prior to c. 1300 CE (50–72%), with sedges becoming more prevalent after c. 1300 CE (22–46%). Charcoal also dramatically drops at this point from 38 to 117 fragments per cm^3 to 3–46 fragments per cm^3. This shift is identified clearly as changes in pollen assemblages (Fig. 3), however, it is not categorised as a statistically significant change in the fungal NPP record. *Zea mays* pollen (Maize) is present in this zone until c. 1400 CE when crop pollen changes to that of *Ipomoea batatas*-type pollen (sweet potato). Organic content is stable throughout the entire core with the percent organic carbon in zone 1 remaining between 6.7 and 8.8%.

4.2.2. Zone NPP-2 (CE 1500–1700 CE)

cf. *Coprinus* sensu lato (10–18%) and *Arthrinium*-type (12–17%) remain the most abundant forms in Zone 2, however their prevalence declines in relation to other forms. Ancillary forms include Xylariaceae form 1 (4–9%) and form 2 (4–17%), Indet. fungal spore 1 (3–10%) and Indet. Ascospore/Basidiospore (2–6%). Fungal NPP concentration declines to 17,620–21,999 (mean = 20,005) spores per cm^3. Pollen in Zone 2 sees a large increase in tree types increasing from <21% in Zone 1 (prior to CE 1503) to consistently between 35 and 40% in Zone 2. Both grasses (22–33%) and sedges (15–23%) decline in proportion. Charcoal remains low (15–36 fragments per cm^3) comparable to levels that have occurred since c. CE 1300. Organic carbon remains low and stable at 7.5–8%. Pollen of sweet potato is occasionally present, along with that of *Inga* sp. a genus containing several species cultivated by pre-Columbian people e.g. 'ice-cream bean' (*Inga edulis*) (Whitney et al., 2014).

4.2.3. Zone NPP-3 (1700–2010 CE)

In the most recent zone (Zone 3) the fungal NPP type Indet. fungal spore 1 (10–25%) continues to increase in proportion although cf. *Coprinus* sensu lato (13–19%) and *Arthrinium*-type (6–11%) remain important. The proportion of Xylariaceae form 1 (3–10%) and form 2 (3–8%) remain similar to that of Zone 2, while *Paradendryphiopsis*-type (4–7%), *Taeniolella*-type (1–6%), *Didymosphaeria*-type (2–5%) and *Phaeosphaeria*-type (0–6%) increase. Fungal NPP concentrations range from 15,805–22,960 (mean = 20,012) spores per cm^3, similar to that of zone 2. Tree pollen continues to increase in its proportion through Zone 3 (36–57%), with sedges and grasses rarely exceeding 20% of the pollen sum. Charcoal continues to remain low (5–29 fragments per cm3) in

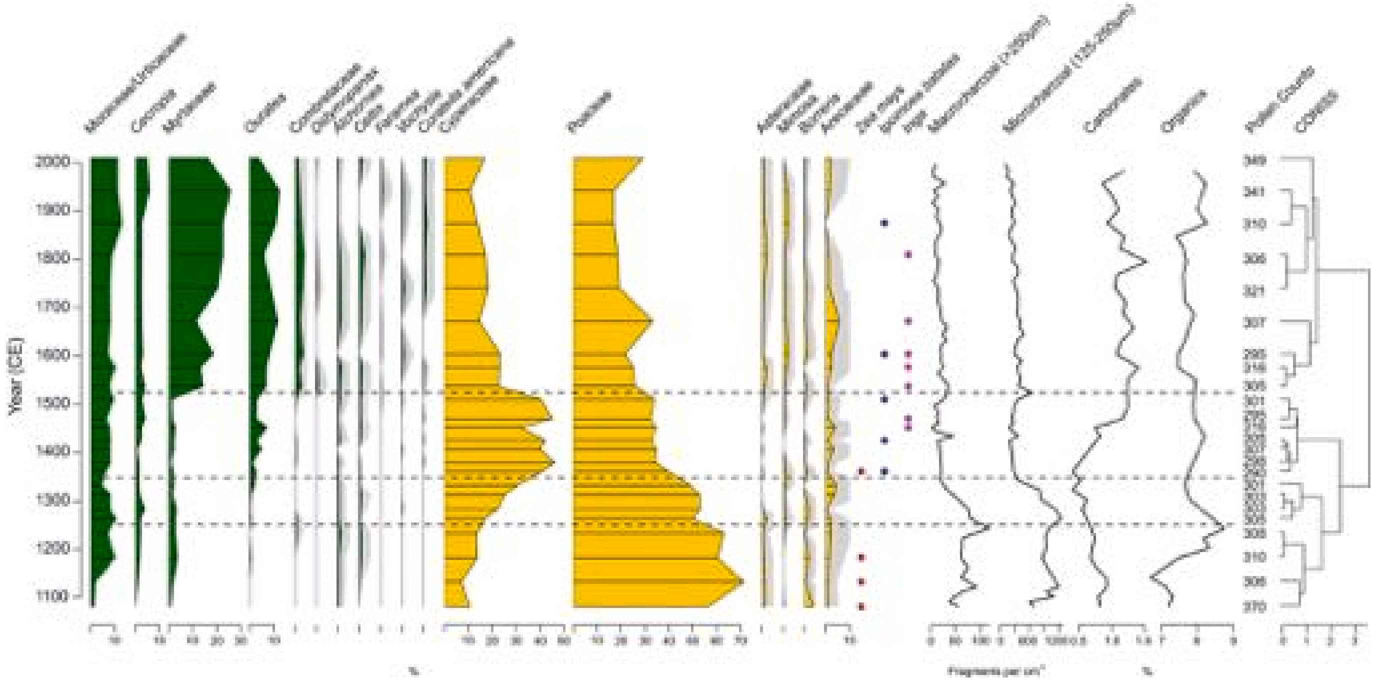

Fig. 3. Pollen data from Whitney et al. (2014) replotted with a new mixed Bayesian age-depth model, loss-on-ignition data, and constrained cluster analysis for pollen data. Coloured dots for cultivars represent a presence at <1% of the pollen sum. Grey shading indicates a 5x magnification of rare taxa. Zone boundaries occur at 63.5 cm (1250 CE), 53.5 cm (1350 CE) and 36 cm (1520 CE).

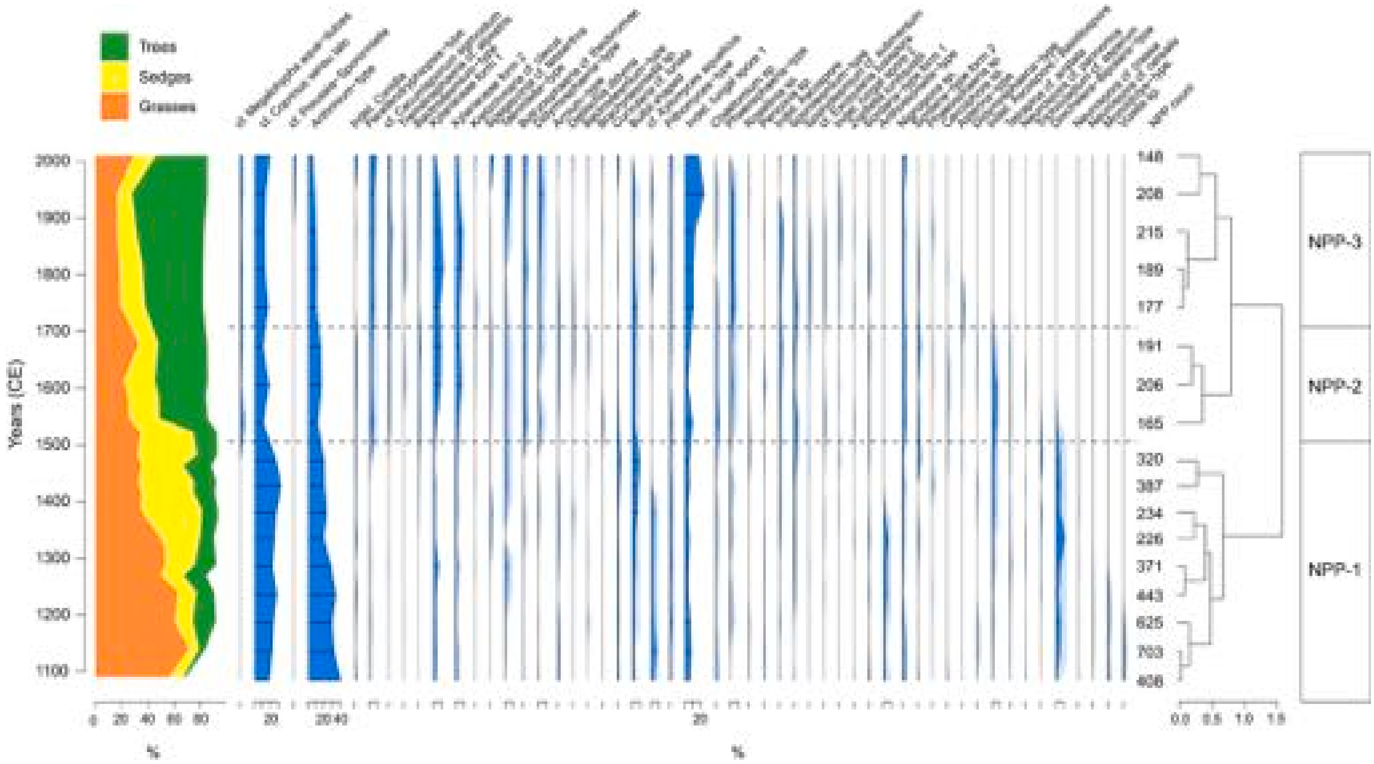

Fig. 4. Fungal NPP plot showing square-root transformed Fungal NPP percentage data with constrained cluster analysis showing statistically significant changes in NPP assemblage. The stacked vegetation plot uses pollen percent data for trees (Moraceae/Urticaceae, Combretaceae/Melastomataceae, Myrtaceae, *Cecropia, Ouratea* and *Celtis*), sedges (Cyperaceae) and grasses (Poaceae). Light blue shading indicates a 5x magnification of rare taxa. Zonal boundaries occur at 37.5 cm (1500 CE) at 22.5 cm (1700 CE). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

levels comparable to that which have occurred since c. 1300 CE. Organic carbon also remains low and stable at 7.4–8.3%.

4.3. Ordinations and permutation tests

The five constrained variables (CCA1-CCA5) account for 56% of the variance in the CCA (constrained inertia = 0.295). With the first two constrained variables (CCA1 and CCA2) having eigenvalues of 0.183 and 0.056, accounting for 35% and 11% of the variance (total inertia = 0.524), respectively. The residual structure, that is explained by the unconstrained variables, constitutes 44% of the variance (unconstrained inertia = 0.223). The first unconstrained variable (CA1) has an eigenvalue of 0.04906 (9%) suggesting that main structure of the data is accounted for in the first two constrained variables. Linear dependencies between the environmental gradients were investigated using VIF. Following the removal of the redundant environmental gradient (grass pollen), all remaining environmental gradients produced a VIF < 5 indicating little collinearity remained.

Analysis of variance (ANOVA) was first used to test the significance of the overall model then that of the individual constrained axis. An F statistic was generated for the observed model (2.829) and compared to that of a null model (mean = 1.036), where species data were randomly reshuffled. ANOVA produced a $P < .001$ (SI Fig. 3a) indicating that 99.9% of the permuted values had an F statistic lower than that of the observed model. A permutation test (ANOVA) for the constrained axis indicated that only CCA1 and CCA2 were statistically significant with $P < .001$ and $P = .006$ respectively, therefore only plots showing the relationship between these first two axis were generated (Fig. 4a).

A reduced model using a stepwise selection method was undertaken which identified the 'tree' and 'sedge' environmental variables as statistically significant. The two constrained axes (CCA1-CCA2) then account for 42% of the total variance (constrained inertia = 0.221), with eigenvalues of 0.169 (32%) and 0.052 (10%) respectively (Fig. 4b). The residual structure therefore constitutes 58% of the variance (unconstrained inertia = 0.303), with the first unconstrained variable (CA1) having an eigenvalue of 0.057 (11%), which is higher than CCA2. Removing the additional environmental variables (organics, fire, cultivars) therefore produces a model where the majority of the environmental signal is unconstrained, suggesting that some of the explanatory power of the initial full CCA has been lost. ANOVA of the reduced model (SI Fig. 3b) produced a higher F statistic (5.099) than for the original model, however, both were statistically significant with a $P < .001$. A permutation test for the constrained axis indicated that both CCA1 and CCA2 were statistically significant with a $P < .001$ and $P = .002$ respectively, while a permutation test for the environmental variables indicated that trees ($P < .001$) and sedges ($P = .029$) were statistically significant under the reduced model.

5. Discussion

5.1. Fungal assemblage shifts

Fungal NPPs are sensitive to changes in local vegetation due to the close relationship between a fungus and its host substrate (Peay et al., 2013), and the small travel distance between where the fungal NPPs are produced and their site of preservation (van Geel and Aptroot, 2006). However, their diverse ecological strategies as saprophytic, parasitic, or mutualistic organisms; the unconstrained ecological affinity of many types; and the difficulty in linking fossil remains to modern taxa leads to uncertainties in interpreting the palaeoecological importance of many types. Therefore, rather than relying on individual taxa to interpret past changes in environment, here an assemblage level approach is used (Loughlin et al., 2018). CONISS and CCA allows for assemblage level changes and the primary environmental drivers controlling the fungal NPP composition to be established without relying on an individual taxa whose specific affinity may be unknown.

The fungal NPP archive records changes in vegetation and human land use surrounding LEC over the last 1000 years, identifying important transitions c. 1500 CE and c. 1700 CE, corresponding to the arrival times of Europeans to the Americas and Jesuit missionaries to the *Moxos* respectively. Multivariate analysis characterises the close relationship between fungal NPPs and local vegetation, as tree cover (tree pollen) and perennially wet areas (sedge pollen) were the significant environmental variables (Fig. 5). Incorporating fungal NPPs into a multiproxy palaeoecological analysis allows for ecosystem changes to be observed that had only a single proxy been used would have been missed, specifically, the assemblage shift at c. 1700 CE (Fig. 4) which was not observable in the pollen signal (Fig. 3). Whilst also corroborating the most significant ecological change in the last 1000 years to have occurred c. 1500–1520 CE, a historically momentous period as the impact of the European invasion and introduction of diseases spread across the Americas leading to the depopulation of the Western Hemisphere.

5.2. Pre-Columbian land-use change

Prior to 1300 CE high abundances of charcoal occur in conjunction with *Zea mays* pollen suggesting that fire played a key role in establishing maize agriculture in the raised-field region (Whitney et al., 2014). The CCA (Fig. 5a) shows that the three earliest fungal NPP samples examined (pre-1200 CE) align strongly along the cultivar environmental variable, however, care should be taken when interpreting this variable due to its qualitative nature, here shown as *Zea mays* presence/absence. Despite the statistical analysis suggesting that the model is not strongly driven by the cultivar and fire environmental variables, several fungal NPP types, *Monodictys*-type, *Vizella* sp. and *Neurospora* cf. *cerealis* are highly correlated with the cultivar variable and only occur prior to 1300 CE (Fig. 5b). *Neurospora* cf. *cerealis* is a fungus found on the crown and roots of cereals and in agricultural soils (Dowding, 1933; García et al., 2004). Here we cannot definitively assign the spores to *Neurospora cerealis*, however, its occurrence only in samples contemporaneous to *Zea mays* pollen supports this identification. *Monodictys*-type is a cosmopolitan genus found on wood, litter, leaves, lichens, soil, algae and in dung (Põlme et al., 2020; Seifert et al., 2011), while *Vizella* sp. are a tropical parasitic leaf fungus and litter saprotroph (Farr, 1987; Põlme et al., 2020). These later types may not immediately be characteristic of agriculture but may provide evidence for future fungal NPP work in the region as they are exclusively present early in the Cerro Phase (1100–1300 CE).

A change from maize cultivation to that of sweet potatoes occurs as burning declines to minimal levels post-1300 CE, perhaps linked to a change in farming method to that of fire suppression (Iriarte et al., 2012). This period sees the first indication of savanna trees appearing, such as *Vochysia* and the fire tolerant *Curatella americana* following their likely clearance during the earlier maize agricultural phase. This in conjunction with Cyperaceae pollen, one of only two statistically significant environmental variables (Fig. 4), surpassing that of Poaceae in abundance may be suggestive of an increase in more permanently wet or

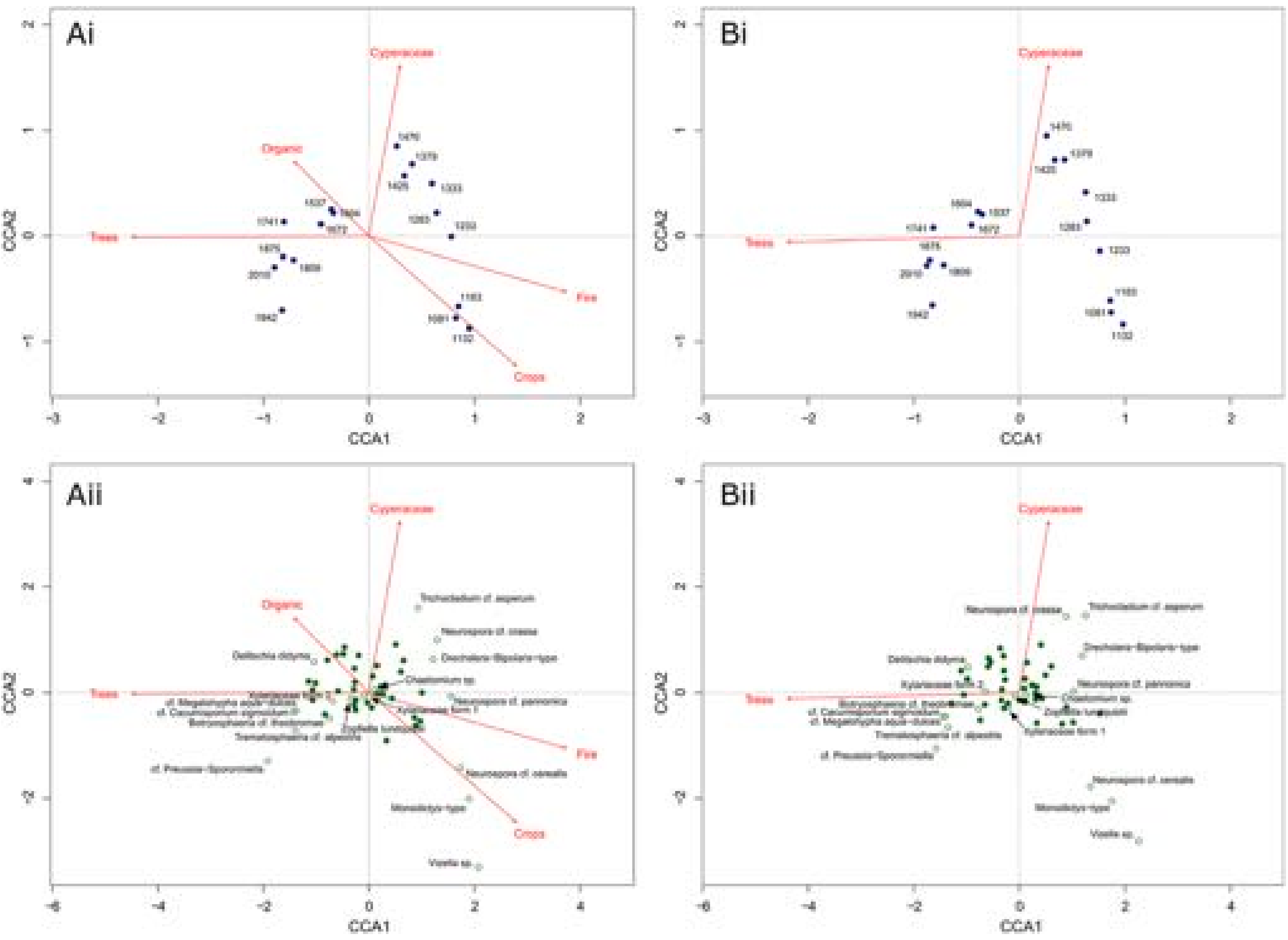

Fig. 5. Full Canonical Correspondence Analysis (CCA) plots for (Ai) samples (dates CE) and (Aii) taxa and reduced (only statistically significant environmental variables) CCA plots for (Bi) samples (dates CE) and (Bii) taxa. Only taxa referred to in the discussion are named (open green dots) other taxa are removed (filled green dots). A full version of plot Aii and Bii with all taxa named can be found in the supplementary information. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Plate 1. Fungal NPP types recorded from LEC. Existing NPP codes and descriptions of new types are included in the Supplementary Information. T1) cf. *Megalohypha aqua-dulces*, T2) cf. *Coprinus sensu lato,* T3) cf. *Preussia-Sporormiella,* T4) *Arthrinium*-type, T5) *Indet. Conidia,* T6) *Paradendryphiopsis*-type, T7) cf. *Cacumisporium sigmoidum,* T8) *Trematosphaeria* cf. *alpestris*, T9) *Bactrodesmium*-type, T10) *Xylariaceae* form 1, T11) *Xylariaceae* form 2, T12) *Spegazzinia* cf. *tessarthra,* T13) *Bactrodesmium*-type, T14) cf. *Xylomyces aquaticus,* T15) cf. *Excipularia fusispora,* T16) *Sporidesmium*-type, T17) *Sporodesmium* cf. *submersum,* T18) *Taeniolella*-type, T19) *Phaeosphaeria*-type, T20) *Phaeosphaeria* sp., T21) *Kretzschmaria* cf. *clavus,* T22) *Periconia* sp., T23) *Brachydesmiella* sp., T24) Bulbil shaped, T25) *Pithomyces*-type, T26) *Delitschia didyma,* T27) *Chaetomium* sp., T28) *Zopfiella lundquistii,* T29) *Rosellinia* sp., T30) *Arnium*-type, T31) *Curvularia* cf. *lunata,* T32) *Botryosphaeria* cf. *theobromae,* T33) *Nigrospora* sp., T34) *Anthostomella*-type, T35) *Tetraploa* cf. *aristate,* T36) *Cercophora* sp. T37) *Asterina*-type, T38) *Sordaria*-type form 1, T39) *Sordaria*-type form 2, T40) *Didymosphaeria*-type form 1, T41) *Didymosphaeria*-type form 2, T42) Indet. Ascospore/Basidiospore, T43) Indet. Ascospore, T44) Indet. fungal spore 1, T45) Indet. fungal spore 2, T46) *Neurospora* cf. *pannonica* (syn. *Gelasinospora*), T47) *Neurospora* cf. *crassa* (syn. *Gelasinospora*), T48) *Neurospora* cf. *cerealis* (syn. *Gelasinospora*), T49) *Drechslera-Bipolaris*-type, T50) *Trichocladium* cf. *asperum,* T51) *Monodictys*-type, T52) *Vizella* sp.

damp ground conditions. Here an increase of *Trichocladium* cf. *asperum* also occurs, which has previously been isolated from various cultivated plant genera, including carrots (*Daucus* sp.), peas (*Pisum* sp.) and potato/tomato (*Solanum* sp.) (Ellis, 1971) and more generally from northern European acidic agricultural soils (Hernández-Restrepo et al., 2017). In this context the presence of *Trichocladium* cf. *asperum* is likely indicative of *Solanum* spp. Throughout the pre-Columbian period *Drechslera-Bipolaris*-type occurs, both fungal genera known as grass pathogens and have been isolated from wheat and oats (Ellis, 1971). It has also been isolated from other grasses, however, despite grasses and sedges remaining above c. 40% of the pollen sum after c. 1500 CE *Drechslera-Bipolaris*-type disappears. Both *Neurospora* cf. *pannonica* and *Neurospora crassa* occur throughout the Cerro Period, including after 1300 CE when charcoal levels are low. *Neurospora* spp. are predominantly pyrophilous (fire-loving) fungi with a life cycle adapted to respond to fire and often found under the bark of burned trees (Jacobson et al., 2006). The presence of these types after 1300 CE despite the lack of charcoal may therefore indicate less intense or limited burning continued to occur but is not observable in the charcoal record.

5.3. *European arrival in the Americas*

In both the fungal NPP and pollen records the most significant change occurs in the 20–30 years post-European arrival in the Americas (1492 CE). The pollen signal shifts to one more characterised by tree taxa, specifically Myrtaceae, which in the *Moxos* is associated with riparian forests. Along with the presence of *Inga* sp. pollen, a genus that contains important semi-domesticated species such as the 'ice-cream bean' tree (*Inga edulis*) (Pennington, 1997). However, *Inga* sp. is also a pioneer in tropical secondary and riparian forests, its increase may therefore be linked to the expansion of riparian forest and not selective cultivation. The distribution of fungal NPP samples along CCA axis 1 (Fig. 4ai - CCA1) exhibits a major change between assemblages from pre-1470 CE to those post-1540 CE. After c. 1500 CE the fungal NPPs associated with cultivation (*Neurospora* cf. *cerealis*, *Trichocladium* cf. *asperum*, *Drechslera-Bipolaris*-type) are absent, replaced by tree pathogens and decomposers such as *Botryosphaeria* cf. *theobromae*, cf. *Megalohypha aqua-dulces*, cf. *Cacumisporium sigmoidum*, *Trematosphaeria* cf. *alpestris* and the Xylariaceae (Burgess et al., 2006; Ferrer et al., 2007; Maharachchikumbura et al., 2016; Põlme et al., 2020). This shift in the fungal NPP assemblage, corroborated by the correlation of these types with the forest pollen variable in Fig. 5, supports a hypothesis of local tree growth and a reduction in cultivation at LEC post c. 1500 CE. However, Whitney et al. (2014) also analysed the pollen of Laguna Frontera, a comparable lake close to LEC where this change to a more forested signal with reduced cultivation appears to have occurred earlier c. 1420 CE based on a new age-depth model (SI Fig. 4). This earlier shift may be linked to local societal level changes in land use prior to European arrival, the lower dating control and variable sedimentation rate at Laguna Frontera, or potentially to larger scale changes in climate as precipitation increased within the Bolivian Andes c. 1450–1550 CE, at the beginning of the Little Ice Age (1450–1850 CE) (Apaéstegui et al., 2018). The extent to which this change in climate from a drier period prior to c. 1450 CE to increased precipitation and potential flooding drove changes in the vegetation of the Moxos and the relative contribution of human hydrological engineering is still uncertain (de Souza et al., 2019).

5.4. *Jesuit arrival in the Moxos*

In 1683 CE Jesuit missionaries arrived to the *Moxos* where the indigenous population had already undergone over a century of depopulation following European arrival (Block, 1994; Koch et al., 2019). The Jesuits introduced cattle farming to the region and encouraged the concentration of indigenous groups into Jesuit-controlled settlements (or reductions) exacerbating indigenous deaths through disease and crop failure (Block, 1994). As Jesuit reductions reached populations of c. 15,000 by 1700 CE, and doubling to c. 30,000 by 1720 CE the cultural landscape of the Moxos changed with the construction of churches, ranches, agricultural complexes, and light industrial plants (Block, 1994). At this time, the fungal NPP assemblage at LEC changes, although, this is not echoed in the pollen record, suggesting that the pollen signal is not sensitive enough to identify this shift in local land-use. Large cattle herds were rapidly established across the *Moxos* by the Jesuits in the early 1700's, so as by the time of their expulsion from the Spanish Empire (1767 CE) mission livestock in the *Moxos* totalled c. 50,000 cattle, not including the freely roaming semi-feral herds which were used as a strategic reserve (Block, 1994). This might be expected to increase the coprophilous fungi found at LEC, however, dung fungus such as cf. *Preussia-Sporormiella* only occur post-1940 CE in small concentrations (200–300 per cm^3), while other coprophilous types e.g. *Delitschia didyma*, *Chaetomiun* sp. and *Zopfiella lundquistii* are found throughout the record. This long term signal of herbivory is expected as the *Moxos* is not devoid of its own native large herbivores with rheas (*Rhea americana*), pampas deer (*Ozotoceros bezoarticus*), capibara (*Hydrochoerus hydrochaeris*) and tapir (*Tapirus terrestris*) present (Langstroth, 2011). The relationship between coprophilous fungi and increases in large herbivores is seen elsewhere in Bolivia, such as in the Andes where *Sporormiella* concentrations at Lake Challacaba spike during the expansion of the Tiwanaku c. 800 CE, linked to the herding of alpaca and llama (Williams et al., 2011). However, at LEC the paucity of coprophilous fungi suggest that large herbivores were never locally abundant enough to be observable using changes in dung fungi. This might be as the LEC core was taken approximately 50 m from the lake edge and *Sporormiella* levels drop off considerably with distance from shore as shown in south-eastern Brazil, where at this distance the presence of small-to medium-herds of cattle appear to have very little influence on the abundance of coprophilous fungi (Raczka et al., 2016). Despite a direct coprophilous fungi signal being absent at LEC, significant changes in the fungal NPP assemblage at c. 1700 CE (Fig. 4), shortly after cattle and horse herds are introduced to the *Moxos*. This change suggests that relying solely on the presence of a signal fungal NPP such as *Sporormiella* may be an over simplistic way of interpreting the NPP record and that a vegetation signal is indeed present c. 1700 CE but in form too subtle for pollen to identify.

6. Conclusions

Palaeoecological analysis of sediments from the seasonally inundated savanna of the *Moxos* identified fifty-two distinct morphological fungal NPP types. Stratigraphically constrained cluster analysis and canonical correspondence analysis show that over the last 1000 years the largest change in the fungal NPP record occurred c. 1500 CE, complementing that of the largest change in the pollen record. This change beginning in the decades following European arrival in the Americas supports the hypothesis that the European Encounter had a profound impact on indigenous land use and the vegetation of the *Moxos* savanna. An additional change in the fungal NPP record, not observed in the pollen record, occurs c. 1700 CE corresponding to the start of Jesuit missionaries' interaction with indigenous groups and the introduction of cattle farming to the region. Fungal NPPs are sensitive to changes in local vegetation due to the close relationship between fungi and their host substrate, and their short travel distance. Assemblage level shifts signal a change in local vegetation that the pollen record is insensitive to, highlighting the risk of relying on a single proxy to interpret vegetation change on multiple scales. Prior to European arrival the fungal NPPs *Neurospora* cf. *cerealis*, *Trichocladium* cf. *asperum* and *Drechslera-Bipolaris*-type, are identified as indicative of indigenous agriculture and offer the ability to expand on the range of plants being cultivated and their temporal range in sedimentary archives. However, more work is needed to improve the identification of these fungal NPPs in modern and past settings. The Laguna El Cerrito record supports incorporating fungal spores into standard palaeoecological analysis as they provide new and complementary information on changes in local vegetation, land use and agriculture.

Author contributions

FEM and BSW conducted the fieldwork; NJDL and BSW designed the research; NJDL and BSW conducted the laboratory work; JMKO, NBNO and NJDL identified the non-pollen palynomorphs; NJDL wrote the manuscript with contributions from all authors.

Funding

Funding for this research was provided through a collaborative partnership between the National Science Foundation (United States) (1758273) and the Arts and Humanities Research Council (United Kingdom) (AH/S00128X/1) through a grant to BSW, JHW and NAD. Fieldwork was funded by a Leverhulme Trust (United Kingdom) research project grant (F/00158/CH) awarded to FEM. Radiocarbon dates were granted by the Natural Environment Research Council radiocarbon facility to FEM (1527.1010/1623.0312).

Declaration of competing interest

None.

Acknowledgments

Fieldwork logistical support was provided by the 'Noel Kempff Mercado' Natural History Museum, Santa Cruz, Bolivia, and 'Programa de Conservación de la Paraba Barba Azul', Trinidad, Beni Department, Bolivia. We also thank Oscar Saavedra for field assistance and to Beatriz Keller de Iriarte and family, and residents of the El Cerro ranch, for their kind hospitality. Thanks go to Encarni Montoya and an anonymous reviewer for their constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2021.105382.

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